The Ecological Role of *Salpa thompsoni* in the Kerguelen Plateau Region of the Southern Ocean: A first comprehensive evaluation

By

Paige Kelly

BMarSc (Hons)

Institute for Marine and Antarctic Studies (IMAS)

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STATEMENTS AND DECLARATIONS

Declaration of Originality

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Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Author 1 (candidate): Paige Kelly, Institute for Marine and Antarctic Studies, Antarctic Climate & Ecosystems CRC, University of Tasmania

Author 2: Dr. Kerrie M. Swadling, Institute for Marine and Antarctic Studies, Antarctic Climate & Ecosystems CRC, University of Tasmania

Author 3: Dr. Jessica Melbourne-Thomas, Antarctic Climate & Ecosystems CRC, University of Tasmania, Australian Antarctic Division

Author 4: Dr. Stuart Corney, Institute for Marine and Antarctic Studies, University of Tasmania

Author 5: Dr. So Kawaguchi, Antarctic Climate & Ecosystems CRC, University of Tasmania, Australian Antarctic Division

Author 6: Dr. Sophie Bestley, Institute for Marine and Antarctic Studies, University of Tasmania

Author 7: Dr. Alexander Fraser, Antarctic Climate and & Ecosystems CRC, University of Tasmania

Author 8: Abigail Smith, Institute for Marine and Antarctic Studies, Antarctic Climate & Ecosystems CRC, University of Tasmania

Author details and their roles:

Paper 1, *Salpa thompsoni* in the Indian Sector of the Southern Ocean: environmental drivers and life history parameters

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Kelly, P., Corney, S., Melbourne-Thomas, J., Kawaguchi, S., Bestley, S., Fraser, A., Swadling, K., (submitted.) Salpa thompsoni *in the Indian Sector of the Southern Ocean: environmental drivers and life history parameters.*

As the candidate, I was responsible for conceiving the research idea, collecting the required information in the field, designing the statistical analyses and writing the original manuscript. Author 6 aided in the construction of the statistical model used in this study and its interpretations. Authors 6 and 7 aided in obtaining historical datasets and in the interpretation of long-term trends identified in this study. Authors 2, 3, 4, 5, 6 and 7 aided in refining research design and implementation, and provided continual advice while the manuscript was being prepared. All contributing authors provided comments on the manuscript.

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As the candidate, I was responsible for conceiving the research idea, collecting the required information in the field, the conception and production of figures and writing the original manuscript. Author 8 undertook the lab component for the gut content analysis and collated the resultant data. Authors 2, 3, 4 and 5 aided in refining research design and implementation, as well as figure production, and provided continual advice while the manuscript was being prepared. All contributing authors provided comments on the manuscript.

We the undersigned agree with the above stated contributions for each of the above submitted peer-reviewed manuscripts contributing to this thesis:

Signed:

Dr. Kerrie Swadling

Primary Supervisor

Institute for Marine and Antarctic Studies

University of Tasmania

Date: Jan 4th 2019

Signed:

Prof. Craig Johnson

Head, Ecology and Biodiversity Centre

Institute for Marine and Antarctic

Studies University of Tasmania

Date:

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GENERAL ABSTRACT

Increasing numbers of gelatinous species may significantly alter the future structure and function of Southern Ocean ecosystems. Most notably, there is evidence of a possible increase in long-term abundance, coupled with a southerly shift in distribution, in the salp *Salpa thompsoni*. Identifying the effects of a potential shift from a *Euphausia superba*-based food web, to a salp-based food web is crucial for quantifying potential ecosystem energy-flow changes, and for facilitating robust approaches to ecosystem-based management. A lack of baseline information on *Salpa thompsoni* biology and ecology (against which to assess change in the ecological role) in the waters off East Antarctica is hampering understanding of the mechanisms underpinning the distribution and dynamics of this species, and therefore preventing researchers from predicting exactly how Southern Ocean salps will behave under forecast environmental change. This thesis examined the abundance and distribution patterns, population structure, environmental drivers, diet, and elemental and nutritional content of *Salpa thompsoni* populations in the Kerguelen Plateau during the 2016 summer. The Kerguelen Plateau is a hotspot for biological productivity, and a location of valuable toothfish fisheries. Furthermore, this thesis investigated the potential for resource overlap between *Salpa thompsoni* and Antarctic krill and compared the in-*situ* energetic potential of the two food sources.

This research found that, during the 2016 summer, *Salpa thompsoni* occurred south of the Southern Boundary of the Antarctic Circumpolar Current (originally considered the southern limit of *Salpa thompsoni* distributions) in higher abundances than previously reported. Using generalised additive models, large blooms were associated with low-chlorophyll-*a* concentration and summer sea-ice retreat. A comparison of the distribution patterns of *Salpa thompsoni* and *Euphausia superba* identified potential for the habitats of the two species to overlap on both horizontal (latitudinal and longitudinal distribution) and vertical (water-column distribution) spatial scales. Evidence for food source overlap was provided by stable isotope and gut content analyses. While salps were once

considered a trophic “dead-end,” improved dietary analysis methods now show *Salpa thompsoni* to be a valid food source for higher predators, albeit with unclear energetic value. In this research, protein and energy content analyses found *Salpa thompsoni* to be an energetically inferior food source for Kerguelen Plateau predators, containing significantly less protein and overall energy than *Euphausia superba*. The findings from this thesis, as well as the resultant datasets on *Salpa thompsoni* population dynamics, will have wide-ranging applications, including incorporation into ecosystem models and future studies on the changing ecosystem role of Southern Ocean salps.

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CHAPTER 1

General introduction, overview of study site and *Salpa thompsoni* biology and ecology, and thesis structure

1.1 Background

Salps (first described as the genus *Thalia* (Browne 1756)), are barrel-shaped, gelatinous plankton, occurring across equatorial, temperate and high latitude waters. Although widely distributed, and, at times, a dominant feature of marine ecosystems, the public and scientific community remain largely unfamiliar with these organisms. One common misconception surrounding salps is that they are close relatives of jellyfish. While both organisms have a transparent body and are of planktonic nature, salps, unlike jellyfish, are chordates and possess a primitive spinal structure. Because of this simplified "backbone," salps are, in fact, a closer relative to humans than jellyfish. In addition, the dorsal nerve cord of salps is considered a potential precursor to the more complex nervous system of vertebrates (Lacalli & Holland 1998). As well as the dorsal nerve cord, major anatomical features of salps include a heart, pharynx, gut, feeding mesh and muscle bands (the number of bands varying with species and life stage). This efficient morphology, and physiology, is highly advantageous and allows for optimal movement, feeding and reproduction.

Salps are considered global indicators of warm water masses (Hereu et al. 2014), and are also associated with low to moderate chlorophyll-*a* (Nishikawa et al. 1995, Nicol

et al. 2000b, Martin et al. 2017). Survival in typically food-poor waters, or under conditions where sufficient feeding opportunities are short-lived, is, in part, due to the salp locomotory mechanism. Salps move using energy-efficient jet propulsion, arising from the expansion and contraction of their muscle bands (Bone & Trueman 1983). This form of locomotion maximises feeding opportunities; drawing potential prey items suspended in the water into the body cavity, and into contact with the feeding mesh. Also aiding salp survival is their ability to ingest a large range of particles (~1-1,000 µm) with 100% efficiency (Bathmann 1988, Fortier et al. 1994, Sutherland et al. 2010). (Note that ingestion of food does not automatically mean that food will be digested; e.g. see Metfies et al. (2014)). A major disadvantage, however, of salps being efficient and indiscriminate suspension feeders, is that they are unable to regulate ingestion rates in food-rich conditions (Deibel 1982, Harbison et al. 1986). Perissinotto and Pakhomov (1998a) identified particle concentrations greater than 1 mg chlorophyll-*a* m^{-3} as dense enough to clog salp feeding mesh, and it was speculated that this "over-feeding" could be partly responsible for the rapid collapse of salp blooms. Alongside their feeding mechanism, a complex reproductive cycle also facilitates salps to maximise their population size during favourable conditions. Salp reproduction alternates between an asexually reproducing "oozoid" solitary, and a sexually reproducing "blastozooid" aggregate. A single solitary is capable of budding off chains of thousands of aggregates, resulting in massive blooms that can contain over 5,000 individuals m^{-3} (Everett et al. 2011).

During periods of peak abundance in the aggregate form, salp biomass can exceed that of typically dominant zooplanktors (e.g. *Euphausia superba* in the Southern Ocean (Piatkowski 1985a, b)). When present in such high abundances, salp chains can become

an alternative prey source for typical predators of copepods and planktonic crustaceans, including Adélie penguins, crabeater seals and common diving petrels. It was originally thought that salps were a trophic "dead-end" (Verity & Smetacek 1996), i.e. not actively consumed by higher trophic level species. This conclusion, however, was largely due to the assumption that an absence of salps in the guts of higher trophic level species was due to a lack of predation (Henschke et al. 2016). As gelatinous organisms tend to rapidly deteriorate once consumed (Arai et al. 2003), gut content analysis, as a stand-alone method, often results in biased diet estimations (Berry et al. 2015). A combination of gut content analysis and advanced diet analysis methods (i.e. stable isotope analysis and DNA markers) have revealed over 200 predators of salps (Henschke et al. 2016). These include commercially harvested temperate fish (Cardona et al. 2012) and crustaceans (O'Rorke et al. 2015), as well as Antarctic fish and seabirds (Yves et al. 2002, Raga et al. 2015).

Providing an additional "menu" choice to higher trophic level species is only one facet of the potential ecosystem effect of increased salp populations. Periods of increased salp production may also alter ocean chemistry and biogeochemical cycling. Cabanes et al. (2017) found the 100 m depth export efficiency of salp fecal pellets to be 2-3 times higher than the majority of sinking particulate organic matter (POM). Consequently, salp waste could provide a significant means of transporting POM between the pelagic and benthic zones. Furthermore, blooms could contribute to depletion of iron in surrounding waters, due to the retention of high amounts of this element in fecal pellets (Cabanes et al. 2017).

Despite the potential for major ecosystem input from salps, current understanding of how populations respond to environmental change, and the extent of their ecological role, is incomplete (Constable et al. 2014, Henschke et al. 2016). Factors attributed to current knowledge limitations include a lack of long-term abundance data (Brotz et al. 2012), overlooking samples or information due to a lack of interest in gelatinous species (Aubert et al. 2018), and the "boom or bust nature" of salps. Geographically, information about salp populations is particularly limited in the Southern Ocean, where open-ocean sampling opportunities are more restricted compared to temperate waters. In addition, the most abundant and southerly distributed Southern Ocean species, *Salpa thompsoni* (first described by Foxton, 1966), is a relatively new discovery in the *Salpa* genus, with the longest-running time-series of its summer abundances commencing in 1993 (see Ross et al. 2014, Steinberg et al. 2015).

There is a suggestion that physical and chemical change in the Southern Ocean is driving both a long-term increase in *S. thompsoni* summer maxima and a southward move in populations (Ross et al. 2014). The irregularity in salp occurrences, and the difficulty in obtaining winter population records, has meant that uncertainty surrounds the ecosystem consequences of shifts in the distribution patterns of *S. thompsoni*. A potential major repercussion of altering *S. thompsoni* range extent is distribution overlap with key Southern Ocean species such as *E. superba*. As changing *S. thompsoni* biomass and distribution patterns are now considered a potential determinant of the future structure and function of the Antarctic and Southern Ocean ecosystem (Alcaraz et al. 2014), knowledge gaps concerning this southern-most occurring salp species require immediate attention.

1.2 *Salpa thompsoni* and the changing Southern Ocean: knowledge gaps

Two salp species occur in the Southern Ocean: *Salpa thompsoni* and *Ihlea racovitzai*, *S. thompsoni* being the focus of this thesis. *Salpa thompsoni* differs from the remainder of *Salpa* species in that it has nine horizontal muscle bands in the solitary form, and, in the aggregate form, six muscle bands, converging towards the centre (Figure 1.1). Depending on growth stage, both solitaries and aggregates can range from approximately 4 to 70 mm in length. The two life stages are distinguished based on body shape: solitaries are tubular, while the more streamlined aggregates have tapered ends, allowing for chain formation. Loeb and Santora (2012) estimate a nine-month life cycle for *S. thompsoni*, with a solitary regeneration time of 7.5 months, and an aggregate regeneration time of 7.5 weeks. Solitary production typically peaks during Autumn (March-April) and aggregate production typically peaks during late Spring/Summer (November-February) (Figure 1.2).

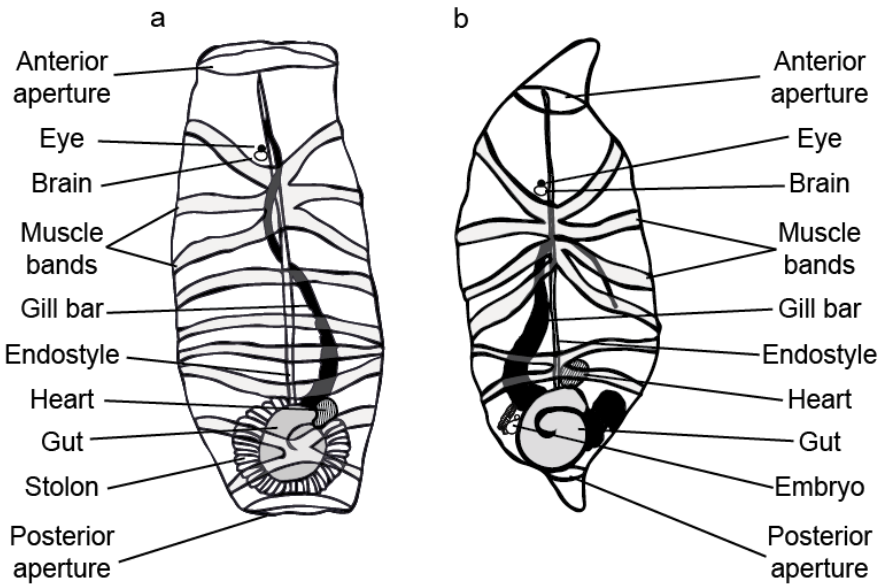


Figure 1.1 Basic anatomy of individual *Salpa thompsoni* mature solitary (oozoid, a) and aggregate (blastozooid, b). When muscle bands expand and contract, water and food are drawn in through the anterior aperture, and water and faeces expelled through the posterior aperture. Immature and developing aggregates contain a partially developed embryo, and immature and developing solitaries contain a partially developed stolon.

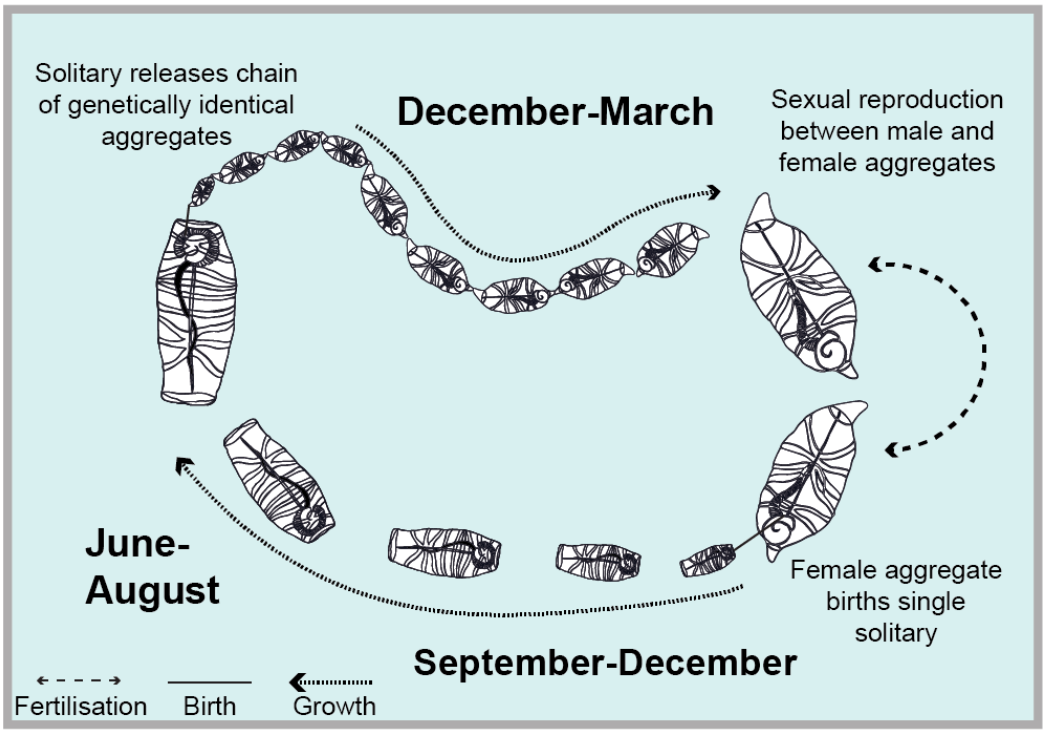


Figure 1.2 *Salpa thompsoni* life cycle, consisting of aggregate (blastozooid) and solitary (oozoid) life phases (modified from Loeb and Santora (2012) and Henschke et al. (2016)). Budding of aggregate chains spans from November-March. Recently released aggregates are female, which are fertilised by older male aggregates. Solitary production spans from December-May. The June-November community primarily consists of overwintering solitaries.

In the foundational study reporting *S. thompsoni* population dynamics, Foxton (1966) noted the species' swarming pattern, unique life history, and the potential for strong annual variation in abundance. In addition, individuals were mostly sampled in sub-Antarctic waters (45 °S-55 °S), and blooms were associated with the warm water masses north of the Southern Boundary Current. The Southern Boundary Current is the southernmost front of the Antarctic Circumpolar Current (ACC), and the southern limit of waters warmer than 1.5 °C. More northern ACC fronts are the Southern Antarctic Circumpolar Current Front (the southernmost limit of water temperatures >1.8 °C), the

Polar Front (the southernmost limit of water temperatures >2 °C), the Subantarctic Front (the southernmost limit of water temperatures >4 °C), and the Subtropical Front (the delineator of subantarctic (to the south) and subtropical (to the north) waters and the southernmost limit of water temperatures >10 °C) (Figure 1.3) (Orsi et al. 1995, Sokolov & Rintoul 2002)).

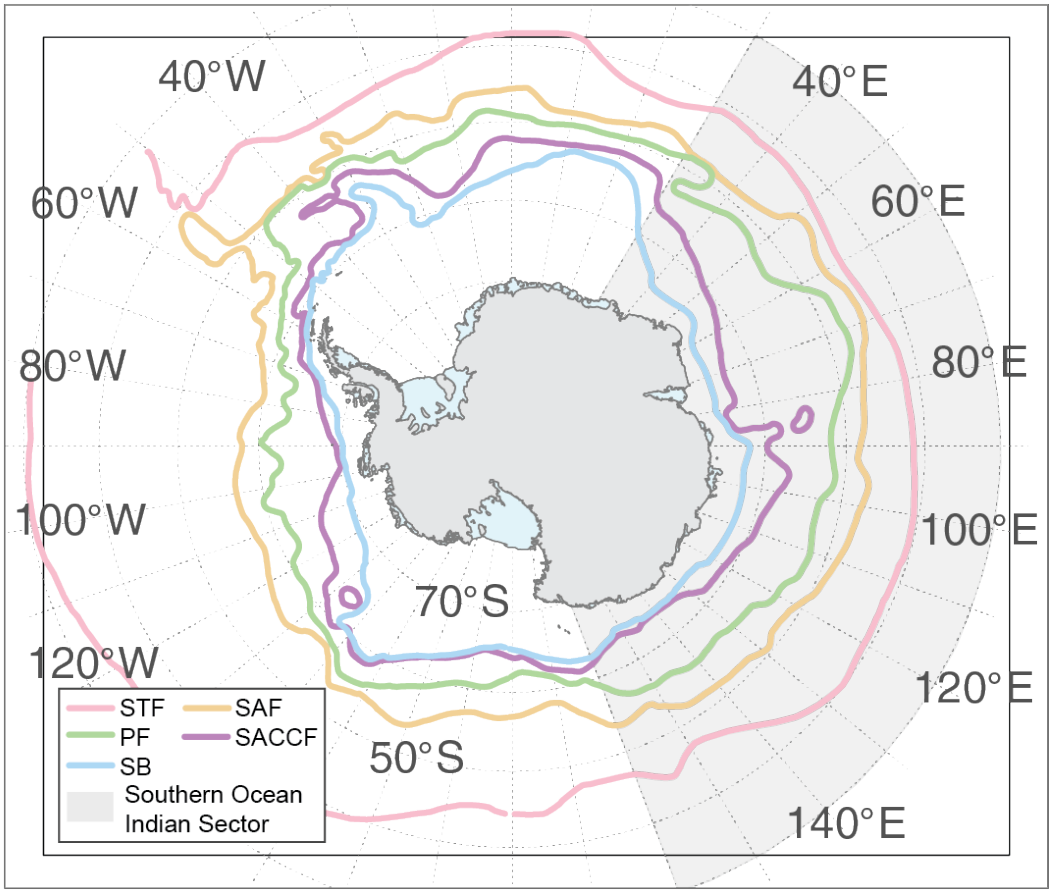


Figure 1.3 Map of Southern Ocean and Antarctica with Antarctic Circumpolar Current fronts (front locations based on (Orsi et al. 1995). STF, Subtropical Front; SAF, Subantarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Current Front; SB, Southern Boundary of the Antarctic Circumpolar Current. The Indian Sector of the Southern Ocean (30°E -160°E) is highlighted in pale grey.

Work following Foxton (1966) focused on reporting basic aggregation and distribution patterns, finding *S. thompsoni* could dominate both the open ocean (Macaulay et al. 1985) and more southerly marginal ice-zone pelagic communities (Torres et al. 1985). With improved understanding of range-extent, studies focused on *S. thompsoni* aggregation and distribution patterns, reporting on diet (Lancraft et al. 1989, 1991), biogeochemical composition (Huntley et al. 1989) and effect on phytoplankton stock (Makarov & Solyankin 1990). Baseline trophodynamic studies found *S. thompsoni* to be an omnivorous feeder, ingesting phytoplankton, protozoans and copepods (Lancraft et al. 1989, Lancraft et al. 1991). It was suggested that blooms of *S. thompsoni* could remove key food sources from the water column, through the ingestion of both copepods and phytoplankton (Makarov & Solyankin 1990). Furthermore, it was speculated that, due to a low food value (Huntley et al. 1989), higher trophic level species were actively avoiding *S. thompsoni* blooms (Ainley et al. 1993).

Temporally regular biological monitoring programs have provided pivotal information on how West Antarctic *S. thompsoni* might be responding to a changing Southern Ocean. Data from the Palmer Long-Term Ecological Research (LTER) region, collected in the waters of the West Antarctic Peninsula (WAP; Figure 1.4), showed a long-term increase in *S. thompsoni* at the continental slope, and a southerly shift in maximum abundances (Ross et al. 2014); data from 1993-2008)). These abundance trends were attributed to a possible movement of warm ACC water closer to the shelf. Other studies have associated increased WAP salp production with preceding winters of decreased sea-ice extent (Atkinson et al. 2004, Ross et al. 2008, Loeb et al. 2009), and a shift from La Niña to El Niño *co*nditions (Loeb & Santora 2012).

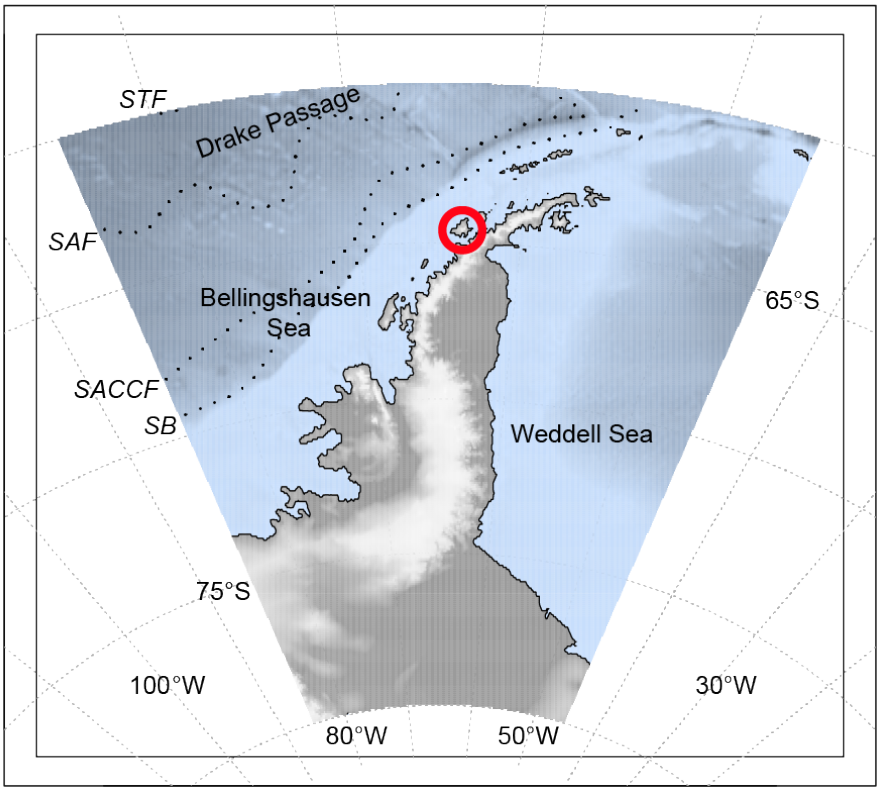


Figure 1.4 Location of the Palmer Long-Term Ecological Research Station (Palmer LTER, red ring). Dashed lines from top to bottom are Antarctic Circumpolar Current fronts (STF, Subtropical Front; SAF, Subantarctic Front; SACCF, Southern Antarctic Circumpolar Current Front; SB, Southern Boundary of the Antarctic Circumpolar Current). The Palmer LETER study annual strategy covers 900 km of the peninsula, with sampling occurring along 200 km long transects (extending west of the coast) at every 100 km.

Despite long-term data collected with Continuous Plankton Recorders, the Indian Sector (30 °E–160 °E) of the Southern Ocean is lacking a consistent time-series for salps. For that region information on *S. thompsoni* is primarily limited to Australian research voyages, with < 20 surveys undertaken in the area over the last 37 years (Australian Antarctic Division 2018). Much of these abundance data have been reported in large-scale syntheses (e.g. Pakhomov et al. 2002), rather than analysed in region-specific studies investigating salp population dynamics. As a result, studies investigating the relationship between salp distribution patterns in the Indian Sector and environmental

conditions (Nicol et al. 2000b, Swadling et al. 2010) are greatly outnumbered by those surveying the waters off the West Antarctic Peninsula (Loeb et al. 1997, Atkinson et al. 2004, Ross et al. 2008, Ross et al. 2014, Steinberg et al. 2015). While both East and West Antarctica are experiencing environmental change (Massom & Stammerjohn 2010, Hill et al. 2013, Constable et al. 2014), there are cross-continental differences in these climatological trends, as well as in the underlying habitat (including the shape and elevation of bedrock beneath ice). Trends in Antarctic sea-ice are particularly spatially variable, with an increase in sea-ice extent observed in the Ross and Weddell Seas and Indian Sector, and a decline observed in the Bellingshausen/Amundsen Seas (Parkinson & Cavalieri 2012). It is crucial to note that, due to the spatial complexity of the Antarctic environment, trends identified in West Antarctic salp populations cannot automatically be applied to the East Antarctic environment. Furthermore, two of the largest-scale East Antarctic surveys (1996 BROKE (Nicol et al. 2000a) and 2006 BROKE-West (Nicol et al. 2010)) highlighted existing small-scale variation in the relationship between the biological community and the environment within the Indian Sector alone. As the Indian Sector is undergoing substantial oceanographic change including a southward shift in the ACC (Fyfe & Saenko 2005), increased discharge from the Wilkes Land ice sheet (Shen et al. 2018) and warming along the northern flank of the ACC (Armour et al. 2016), the local zooplankton community composition, and trajectory of salp biomass, may be rapidly shifting.

Recent sampling of summer *S. thompsoni* populations in the Indian Sector has found that, along 140 °E, the species is capable of completing its lifecycle south of the Southern Boundary of the ACC (Ono & Moteki 2017). If, as observed for *S. thompsoni* in the WAP, Indian Sector *S. thompsoni* are shifting southward, flow-on effects may

eventuate in a permanently altered ecosystem structure and function. One means through which ecosystem structure may alter is if increased salp biomass affects the behaviour and distribution patterns of *E. superba*. Based on West Antarctic dominance patterns, *E. superba* and *S. thompsoni* rarely co-exist in high abundances (Pakhomov et al. 2002, Steinberg et al. 2015). Instead, the zooplankton community see-saws between years of salp dominance ("salp years") and years of krill dominance ("krill years") (Ross et al. 2014). In addition, there is usually pronounced spatial segregation between krill and salp populations (Nicol et al. 2000b, Atkinson et al. 2004). Concerning the mechanisms supporting krill versus salp prevalence, there is evidence that temperature, sea-ice and chlorophyll-*a* drive large-scale population segregation of *S. thompsoni* and *E. superba* in the Indian Sector (Nicol et al. 2000b). The direct effect of increased *S. thompsoni* presence on *E. superba* populations, however, is unknown. Aspects of Indian Sector *S. thompsoni*/*E. superba* interactions requiring further study include the potential for diet and fine-scale habitat overlap, and whether such overlap is causing *S. thompsoni* to displace *E. superba*. For a complete understanding of whether *S. thompsoni* actively competes with other zooplankton, or whether it is simply an opportunistic species, we require up-to-date findings on how *S. thompsoni* populations are responding to variability and change in the Indian Sector environment.

Changes in *E. superba* behaviour and distribution patterns that are mediated by increased presence of *S. thompsoni* may, in turn, alter the population dynamics of fish, squid, whales, seals, penguins and seabirds that rely on *E. superba* as a primary food source. West Antarctic *S. thompsoni* possess less than one third of the energetic content of West Antarctic *E. superba* (Färber-Lorda et al. 2009, Dubischar et al. 2012), meaning that, during "salp years" in that region, the staple food source on offer to higher trophic

level species is a low quality food option. How higher-trophic levels species are responding to increased *S. thompsoni* presence is not entirely understood. A region-specific nutritional profile using *S. thompsoni* and *E. superba* from the Indian Sector is required to determine whether there is a substantial energetic imbalance between the two food sources in the region. A localised nutritional profile, together with information on Indian Sector *S. thompsoni* trophic relations and environmental responses, will provide an essential platform for investigating the ultimate effect of "salp years" on higher trophic levels species and ecosystem energy flow (the amount of energy transferred throughout the food web through consumption). As the physical and chemical characteristics of the Southern Ocean continue to change, an improved understanding of the trophic role of *S. thompsoni* in the Indian Sector is essential to help maintain the structure and function of the surrounding ecosystem.

1.3 Study region: The Kerguelen Plateau, Indian Sector of the Southern Ocean

The Australian Antarctic Territory consists of all islands and territory south of 60 °S, between 45 °E and 160 °E (excluding the French Territory of Adélie Land, which divides the territory into East and West regions). From the baseline of this territory, Australia's most southern Exclusive Economic Zone extends 200 nautical miles into the Indian sector of the Southern Ocean. The Kerguelen Plateau is situated in this EEZ, at approximately 55 °S, 75 °E. A major bathymetric feature of the Southern Ocean, the Kerguelen Plateau is the largest single obstacle in the path of the ACC (Bestley et al. 2018). ACC transport may divert north of the plateau, or pass through the Fawn Trough (a deep channel dividing the plateau into north and south) (Belkin & Gordon 1996, Vivier

et al. 2015). At the southern end of the plateau, the Southern Antarctic Circumpolar Front and the Southern Boundary of the ACC pass through the Princess Elizabeth Trough (Orsi et al. 1995, Sokolov & Rintoul 2009). As a result of interaction between the ACC fronts and the Kerguelen Plateau, the region experiences major upwelling events, leading to increased mixed-layer nutrients and iron flux (Moore & Abbott 2002, Sokolov & Rintoul 2007). Consequently, the waters of the Kerguelen Plateau region are home to complex phytoplankton blooms (Priester et al. 2017), and serve as a highly significant region of primary productivity in the Southern Ocean (Arrigo et al. 2008).

The high primary productivity of the Kerguelen Plateau region supports higher trophic levels of great commercial value, with toothfish (*Dissostichus eleginoides*) and icefish (*Champsocephalus gunnari*) fisheries operating in the northern waters (Duhamel & Welsford 2011). These Southern Ocean commercial fisheries contribute to industries valued at over $USD 6 million (value of CCAMLR-regulated icefish fisheries (CCAMLR Secretariat 2016)) and $USD 50 million (value of Australian-operated toothfish fisheries (Savage 2015)). The Kerguelen Plateau is also an area of significant ecological value, with high krill biomass to the south (Pauly et al. 2000, Nicol 2006), and higher order predators, including seabirds and whales, using the plateau for migration and feeding (Patterson et al. 2016, Bestley et al. 2018).

Prior to 2016, the BROKE and BROKE-West surveys were the only two research voyages to survey the zooplankton biology of the Kerguelen Plateau region. The two surveys sampled the lower Kerguelen Plateau community, south of 62 °S (Nicol et al. 2000b, Swadling et al. 2010). While the primary biological focus of these surveys was to describe *E. superba* abundance and distribution patterns, *S. thompsoni* was sampled at

some stations, and potential environmental drivers behind these blooms were elucidated. The most recent research voyage to survey the Kerguelen Plateau was the 2016 KAXIS Voyage, which sampled the zooplankton community at 40 locations between 57.6 °S and 65.5 °S and 73.3°E and 93.6 °E (Figure 1.5). The KAXIS sampling bounds encompassed an oceanographically complex region, and the voyage provided a unique opportunity to investigate species' distribution, and population transport, within multiple zones, including the ice-edge, the Southern Boundary of the ACC and the Southern ACC Front. Compared to the BROKE and BROKE-West surveys, which were orientated around species-specific (*E. superba*) research objectives, the KAXIS research objectives were ecosystem-focused, aiming to identify and spatially distinguish *E. superba*-based and copepod-based food webs, and determine the biophysical conditions driving food webs of alternate structure (SOKI-Wiki 2016). Information on *S. thompsoni* distribution patterns, population dynamics and trophodynamics, collected as part of the KAXIS voyage, are the main data input for this thesis.

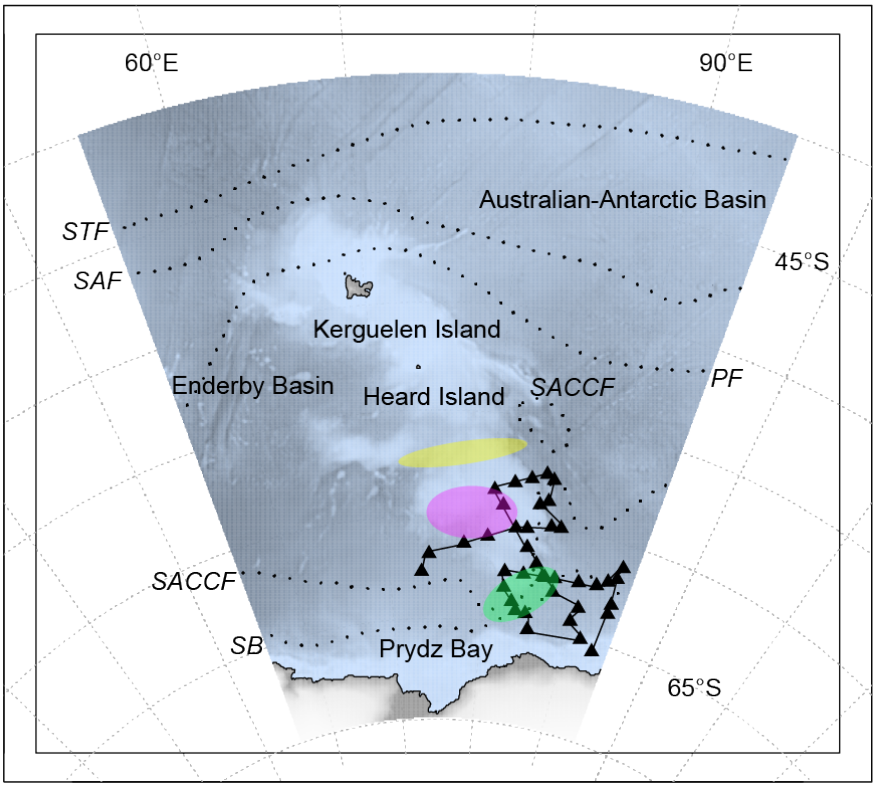


Figure 1.5 Kerguelen Plateau and surrounding major bathymetric and oceanographic features. STF, Subtropical Front; SAF, Subantarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Current Front; SB, Southern Boundary of the Antarctic Circumpolar Current. The yellow shaded area south of Heard Island represents the Fawn Trough, pink shaded area south of the Fawn Trough covers the region of the BANZARE Bank and the green shaded area south of the Banzare Bank covers the region of the Princess Elizabeth Trough.

1.4 Thesis outline and approach

This research provides the first comprehensive account of the ecosystem role of *Salpa thompsoni* in the Kerguelen Plateau region of the Indian Sector of the Southern Ocean (Figure 1.6). This research on *S. thompsoni* biology and ecology encompasses abundance and distribution patterns, population structure (life stage, size and maturity phase), population responses to environmental variables, potential horizontal and vertical

habitat overlap with *E. superba*, potential food source overlap with *E. superba*, elemental and stable isotope composition, and energetic potential.

- **Chapter 1** describes salp and *S. thompsoni* morphology and life history, as well as presenting existing knowledge of *S. thompsoni's* role in the ecosystem. This chapter also details the oceanographic and biological significance of the Kerguelen Plateau region, highlighting the scarcity of sampling for *S. thompsoni* in the Indian Sector of the Southern Ocean, and the uncertainty surrounding the environmental conditions that encourage *S. thompsoni* blooms.
- **Chapter 2** presents information on *S. thompsoni* density, distribution and population structure, collected across the southern Kerguelen Plateau, from January-February 2016. The *S. thompsoni* distribution data showed that 2016 maxima were larger, and occurred further south, than maxima sampled during Indian Sector surveys in the past. This chapter also establishes *S. thompsoni* population-environment relationships. Using a suite of environmental variables, Generalised Additive Models identified the major drivers of *S. thompsoni* blooms as reduced latitudinal sea-ice extent and low chlorophyll-*a*. The role of sea-ice retreat in *S. thompsoni* bloom formation was also supported by long-term observations (20+ years) of latitudinal sea-ice extent across the Indian Sector of the Southern Ocean. A potential consequence of increasing or southerly shifting *S. thompsoni* blooms is resource overlap with *Euphausia superba* (Siegel & Nicol 2008).
- **Chapter 3** assesses the potential for habitat overlap across the Indian Sector of the Southern Ocean over 30+ years, as well as the potential for recent food

source overlap in the Kerguelen Plateau region. A combination of routine (pre-planned) and target (opportunistic) trawls suggested that 2016 Kerguelen Plateau *S. thompsoni* and *E. superba* overlapped on both horizontal and vertical scales. Gut content analysis also revealed that Kerguelen Plateau *S. thompsoni* can ingest the entire range of *E. superba* prey sources. Furthermore, stable isotope analysis was used to explore niche overlap, suggesting that the trophic position of *S. thompsoni* was more similar to *E. superba* than other Southern Ocean euphausiids. In regions of overlapping *S. thompsoni* and *E. superba* habitat, *S. thompsoni* may present itself as an alternative food source for typical *E. superba* predators.

- **Chapter 4** reports elemental and energetic profiles for 2016 Kerguelen Plateau *S. thompsoni* and *E. superba* and demonstrates how *S. thompsoni* (based on protein and energy content) is an inadequate prey source for typical euphausiid and copepod predators. Using the protein and energy profiles of this study, this chapter also compares the number of individual *E. superba* and *S. thompsoni* required to satisfy the metabolic needs of three Southern Ocean penguin species, and discusses how a potential predator might employ optimal foraging strategies when presented with an *S. thompsoni* bloom.
- **Chapter 5** discusses whether it is practically possible for euphausiid predators to satisfy their metabolic needs by feeding exclusively on *S. thompsoni*, as well as the potential effect of increased feeding on *S. thompsoni* (whether it be passive or predatory) on ecosystem energy flow. The current heightened interest in trends in marine gelatinous species is also commented on, and how mainstream media reports influence both research directions and common

perception of what marine species occurrences indicate in regard to ecosystem change. Finally, a synthesis of the findings from this work is presented, discussing immediate applications for data (i.e. models used in ecosystem management), and how this research will serve as a foundation for future studies quantifying potential *S. thompsoni*-driven changes in higher-order predator biomass and ecosystem energy flow.

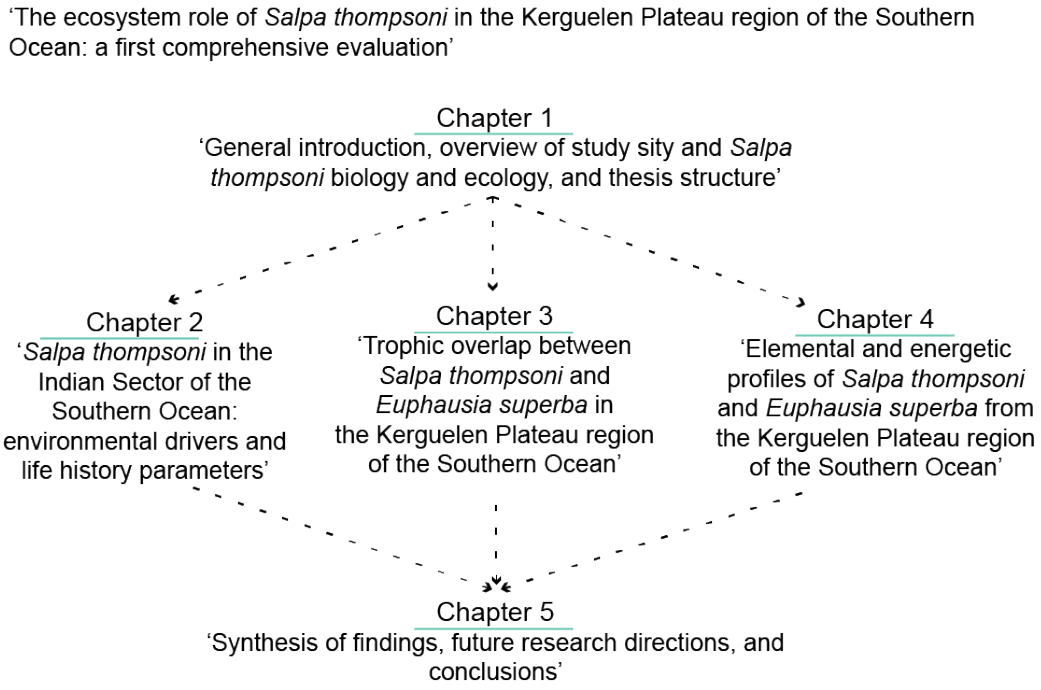
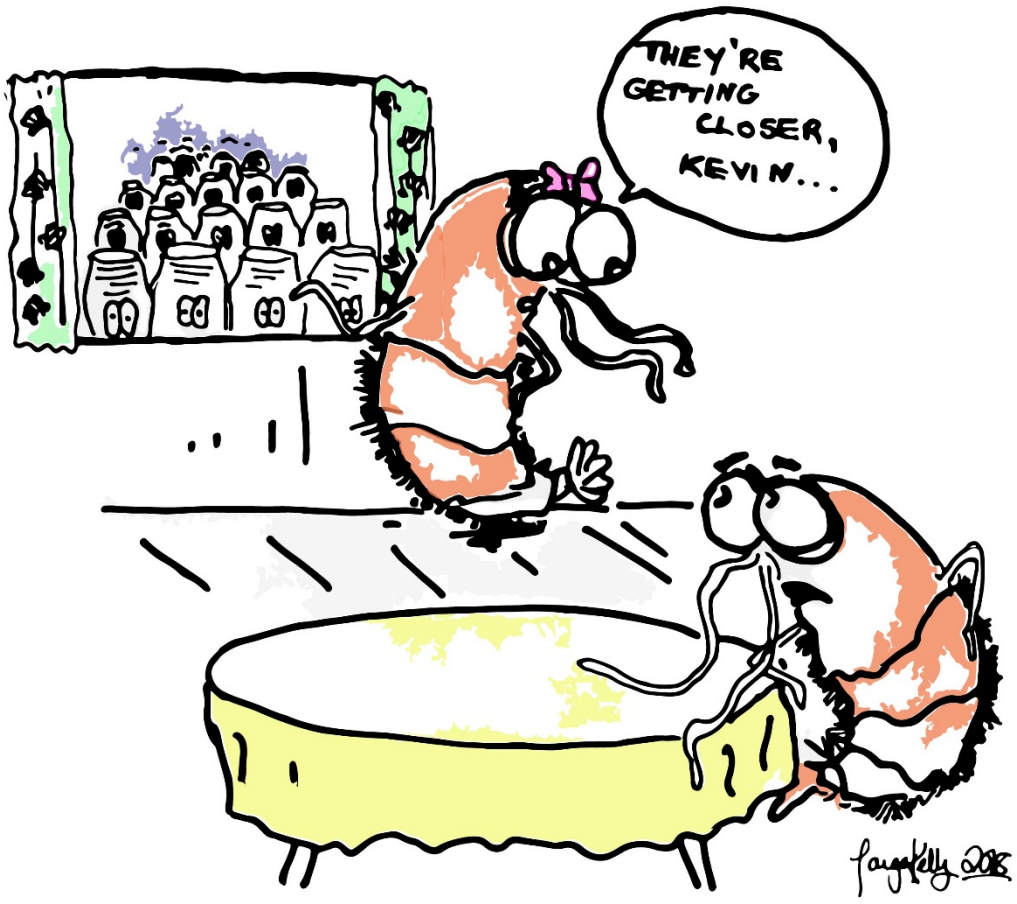


Figure 1.6 Thesis outline.


THEY'RE GETTING CLOSER, KEVIN...

CHAPTER 2

Salpa thompsoni in the Indian Sector of the Southern Ocean: environmental drivers and life history parameters

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Preface:

The Southern Ocean ecosystem is thought to be experiencing a long-term increase in Salpa thompsoni*. Uncertainty surrounds the environmental drivers behind changing abundances of* S. thompsoni*, particularly within the East Antarctic region. For this chapter,* S. thompsoni *populations were sampled in the Indian Sector of the Southern Ocean, as part of the 2016 Kerguelen Axis (KAXIS) voyage. Observations from this voyage were compared with historical abundance records from the broader Kerguelen Plateau region from voyages during 1985-2006. Results show that in 2016 maximum* S. thompsoni *densities across the Kerguelen Plateau were higher, and located further south, than those previously sampled in the area. The highest 2016* S. thompsoni *densities exceeded 2,500 individuals 1,000 m^{-3} and were located between the Southern Boundary of the Antarctic Circumpolar Current Front and the Southern Antarctic Circumpolar Current Front. Generalised Additive Models associated low chlorophyll-*a *concentration with higher* S. thompsoni *densities. In addition, elevated abundances occurred around eight weeks after sea-ice retreat. These abundance-environment relationships are consistent with results from previous surveys in the region, as well as studies in the West Antarctic region. The new information from this chapter provides much needed baseline abundance and distribution data (which can be used to assess future change in a currently understudied oceanographic region) on a species that may play an increasingly important role in ecosystem structure and function in the Indian Sector of the Southern Ocean.*

2.1 Highlights

- In January/February 2016, Kerguelen Plateau *S. thompsoni* densities were higher, and maximum densities were located further south, than those previously sampled in the region.
- Based on Generalised Additive Models, sea-ice retreat, lower light conditions and lower productivity were associated with higher densities of *S. thompsoni* in 2016. Mechanisms behind these significant density/environment relationships might include diel vertical migration by *S. thompsoni* and melting sea-ice causing a shift in the phytoplankton community composition.
- During Kerguelen Plateau region surveys prior to the 2016 KAXIS voyage, sea-ice melt may also have been a driver of *S. thompsoni* blooms, with higher densities coinciding with lower latitudinal sea-ice extent.
- The KAXIS data form a comprehensive set of baseline information against which to assess future changes in densities, distribution patterns and population dynamics, in Kerguelen Plateau region *S. thompsoni* populations.

2.2 Key words

Salpa thompsoni, Kerguelen Plateau, zooplankton distribution patterns, lower trophic level assemblages, zooplankton life history.

2.3 Introduction

Zooplankton graze on primary producers (e.g. photosynthetic algae) and are themselves food for secondary and tertiary level consumers (e.g. fish). Through these predator-prey interactions, zooplankton provide an essential pathway for energy flow

from low to high trophic levels in marine ecosystems. In the Southern Ocean, efficient energy transfer relies heavily on the macrozooplankton *Euphausia superba* (Antarctic krill), which is a highly nutritious food source (Atkinson et al. 2002, Färber-Lorda et al. 2009, Meyer et al. 2010) consumed by fish, squid, whale, seal and penguin species. Distribution patterns and abundances of *Euphausia superba* are associated with increased year-round sea-ice extent (Flores et al. 2012b), low winter sea-surface temperature (SST) (Fielding et al. 2014) and increased chlorophyll-*a* (Steinberg et al. 2015).

In the West Antarctic, *Salpa thompsoni* has replaced *E. superba* as the dominant macrozooplanktor during summers when conditions are unfavourable for *E. superba* (Lee et al. 2010, Loeb & Santora 2012); i.e. years with decreased winter sea-ice extent (Atkinson et al. 2004) and increased summer sea-surface temperatures (Lee et al. 2010, Steinberg et al. 2015). *Salpa thompsoni*, the most abundant Southern Ocean salp species, is a barrel-shaped tunicate, with a very different chemical composition, feeding mechanism and life history from *E. superba* (Sutherland et al. 2010, Dubischar et al. 2012, Loeb & Santora 2012). The reproductive cycle of *S. thompsoni* —which allows for massive blooms to occur—is distinctive: alternating between a sexually reproductive "aggregate" phase, and an asexually reproducing "solitary" stage (Foxton 1966, Loeb & Santora 2012).

If predicted climate change scenarios (Pachauri et al. 2014) are realised, then the reproductive success of *E. superba* is projected to decline substantially by the year 2100 (Kawaguchi et al. 2013, Piñones & Fedorov 2016). Whether *S. thompsoni* will occupy the niche vacated by *E. superba* under such future conditions, and to what extent this trophic shift would alter the energy budget and flow within the Southern Ocean

ecosystem, remains unclear (Constable et al. 2014, Steinberg et al. 2015). To improve understanding of the potential ecosystem role of *S. thompsoni* in the Southern Ocean, changes in the distribution patterns of *S. thompsoni*, and the environmental conditions driving high abundances, must be clarified on a circumpolar scale. Currently, information about *S. thompsoni* is concentrated in the West Antarctic region, with recent studies investigating multiple aspects of the ecology and biology of *S. thompsoni*, including distribution patterns, genetic composition and life history (e.g. Loeb & Santora 2012, Ross et al. 2014, Steinberg et al. 2015, Batta-Lona et al. 2017). Conversely, relatively few studies over the last decade have provided information on seasonal *S. thompsoni* abundances in the Indian Sector of the Southern Ocean (Carlotti et al. 2008, Takahashi et al. 2011, Pavithran et al. 2012, Ono & Moteki 2013).

The Indian Sector of the Southern Ocean is a region susceptible to major oceanographic and ecological change, with environmental pressures including the thinning of East Antarctic glaciers (Pritchard et al. 2012, Khazendar et al. 2013) and warming along the northern boundary of the Antarctic Circumpolar Current (ACC) (Armour et al. 2016). Anthropogenic pressures may also soon increase, with the reestablishment of a commercial *E. superba* fishery in the region (CCAMLR 2018b). Under such stressors, the influence of gelatinous species, such as *S. thompsoni*, on the future structure and function of the Indian Sector ecosystem may increase. Spatial information on distribution patterns of *S. thompsoni*, and its relationship with oceanographic conditions in the region, is needed to help understand the likely response of *S. thompsoni* to a changing climate.

In this study, life history and abundance data of *S. thompsoni*, collected around the southern end of the Kerguelen Plateau from January-February 2016, was used

investigate recent population dynamics in the Indian Sector of the Southern Ocean. Historical abundance data from research voyages undertaken during 1985-2006 within the broader Kerguelen Plateau region were also collated to provide a long-term context for interpreting the 2016 data. This chapter addresses the following questions:

1. How do 2016 summer distribution patterns of *S. thompsoni* compare with historical data from the Kerguelen Plateau region?

2. What environmental conditions have driven 2016 summer *S. thompsoni* blooms in the Kerguelen Plateau region?

3. How have abundances of *S. thompsoni* in the Kerguelen Plateau region changed over time, under varying winter sea-ice and summer SST conditions (examined using records over the period 1992-2016)? Do results support the hypothesis of *S. thompsoni* blooms being driven by decreased winter sea-ice (Atkinson et al. 2004), or ACC-driven temperature changes (Ross et al. 2014)?

4. Are the identified abundance-environment relationships and trends in distribution patterns consistent with observations from long-term West Antarctic studies (e.g. Loeb & Santora 2012)?

Findings from this study will improve quantitative predictions concerning future abundances of *S. thompsoni* under changing Southern Ocean conditions, and the potential for this species to alter energy flow in the Indian Sector of the Southern Ocean. The life history and population response information in this chapter will also serve as a foundation for future research into identifying potential long-term change in *S. thompsoni* abundances and distribution patterns in the Indian Sector of the Southern Ocean, as well as research into east-west comparisons of *S. thompsoni* bloom drivers.

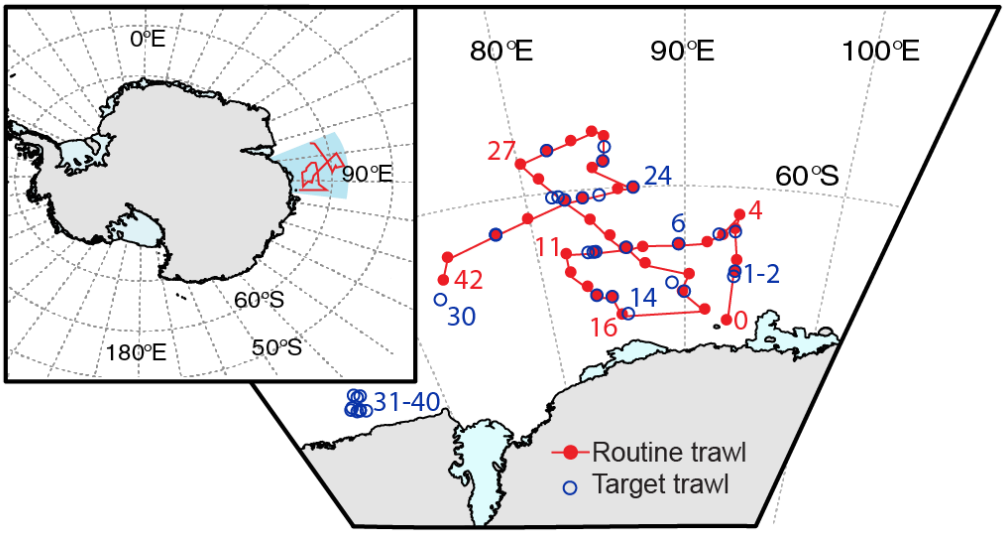
2.4 Methods

2016 Kerguelen axis (KAXIS) Salpa thompsoni *sampling locations and field methods*

During January-February 2016, the Kerguelen Axis (KAXIS) marine science voyage sampled the zooplankton community (through routine rectangular midwater trawls (RMT8)) at 40 locations across the southern Kerguelen Plateau, in the Indian Sector of the Southern Ocean (Fig. 2.1, Table A1.1, Table A1.2). The voyage track crossed the Southern Boundary of the Antarctic Circumpolar Current (SB) and the Southern Antarctic Circumpolar Current Front (SACCF), with trawl locations concentrated in the region of the sea-ice edge near the Princess Elizabeth Trough, and the Southern BANZARE Bank between 70 ^{o}E and 91 ^{o}E. *Salpa thompsoni* were collected using an RMT8 net (Baker et al. 1973), with an 8 m^2 mouth diameter, and a 4.5 mm mesh size. Net deployments were classified as either "routine" (pre-planned) or "target" (opportunistic). Routine trawls were oblique tows, providing an integrated sample from 200 m to near surface (Table A1.1). Routine trawl duration was 20-45 minutes, with each trawl covering an average horizontal distance of 1,200 m. Target trawls sampled approximately a 10-25 m depth range over 5-15 minutes duration. These were directed at an identified acoustic target (using the 38 and 120KHz frequencies of calibrated Simrad EK60 scientific echo-sounders; Horten, Norway) suggesting the presence of an *E. superba* swarm (Table A1.2). For 20 of the 40 routine trawls, and 7 of the 27 target trawls, a random subset of *S. thompsoni* was sampled. Trawls were selected for subsampling based on whether *S. thompsoni* were present and in sufficient condition, and whether, at the time, recording immediate morphometrics of fresh individuals (which provide more accurate body parameter estimates than preserved individuals) was logistically possible.

Morphometrics (total length, oral-atrial length, gut diameter) along with life stage and maturity stage were recorded immediately after collection. Where possible, the morphometrics of 20-50 individuals were recorded per trawl. Life stages were determined by observing the ovaries of each individual and by referring to the length-maturity guide in Loeb and Santora (2012) (originally presented by Foxton (1966)). The life stages reported for aggregates and solitaries in this study—immature, developing and mature—correspond to small, medium and large, respectively, in Loeb and Santora (2012).

Figure 2.1 (left) Location of Kerguelen Axis study region (red trail on blue shaded area)



with respect to the Antarctic continent and (right) Kerguelen Axis voyage track. Trawl locations are denoted by red circles connected by lines (routine) and blue rings (target). Select trawls are numbered to clarify voyage path.

Historical Salpa thompsoni *routine trawl abundance data*

A time series of *S. thompsoni* abundances (reported as densities: individuals 1,000 m^{-3}) was compiled for the broader south Kerguelen Plateau region (58 °S–70 °S, 70 °E–105 °E) from historical data (i.e., occurring prior to the Kerguelen Axis voyage, Table

A1.3). Data were obtained if samples were collected during an approximately 200 m deep oblique tow using an RMT8 net, and if the tow occurred between October and March. We used historical data from SIBEX II (January 1985, n = 29 trawls (RMT 8 zooplankton data from the SIBEX I voyage were not available)) (Hosie 1999, updated 2017c), AAMBER (March 1987, n = 22 trawls) (Hosie 1999, updated 2014b), AAMBER II (January/February 1991, n = 51 trawls) (Hosie 1999, updated 2014a), KROCK (January/February 1993, n = 42 trawls) (Hosie 1999, updated 2017b), BROKE (January-March 1996, n = 66 trawls) (Hosie & Nicol 2000, updated 2017) and BROKE-West (January-March 2006, n = 16 trawls) (Swadling & Kawaguchi 2007, updated 2017) (Table A1.3).

Multi-decadal winter meridional sea-ice and summer SST

Historical and KAXIS *S. thompsoni* abundances (reported as densities: individuals 1,000 m^{-3}) were compared against long-term meridional winter sea-ice extent and summer SST data, to examine the hypotheses that increased numbers are driven by decreased winter sea-ice (Atkinson et al. 2004) and/or increased summer ocean temperatures (Ross et al. 2014). Densities were compared as is, with no statistical analysis method applied due to the temporal inconsistency of *S. thompsoni* sampling. Satellite data were compiled for the region between 70 °E and 105 °E, over the period 1992-2016. Annual winter meridional sea-ice extent was calculated from the SSM/I satellite sensor processed using the Artist Sea-Ice (ASI) algorithm (Kaleschke et al. 2001, Spreen et al. 2008). Annual winter statistics of the meridional sea-ice extent comprised averaged June, July and August 12.5 km resolution data. Presence of sea-ice was classified as pixels with above 15% concentration. These data (Kaleschke et al. 2014) are

publicly available from the University of Hamburg (ftp://ftp.icdc.zmaw.de:/asi_ssmi_iceconc/ant). Monthly SST data are from the NOAA Optimum Interpolation Sea Surface Temperature V2 product (Reynolds et al. 2002), available at 0.25° spatial resolution (https://www.esrl.noaa.gov/psd/). Annual summer statistics comprised averaged data from January and February of a given year (e.g. 2016) and the preceding December (e.g. 2015).

In-situ environmental variables from the 2016 Kerguelen Axis voyage: chlorophyll-a, solar elevation, mixed layer depth, temperature minimum and buoyancy

A suite of environmental data was obtained from the KAXIS oceanographic stations associated with each RMT trawl. The oceanographic measurements were sampled to WOCE accuracy using a SeaBird SBE911plus Conductivity-Temperature-Depth sampler, mounted on a SeaBird rosette with 24 x 10 litre General Oceanics Niskin bottles (Rosenberg & Eriksen 2016). Physical oceanographic variables examined were average salinity from 0-200 m (PSU), the temperature minimum from 0-200 m (or remnant "winter water", °C), the Brunt–Väisälä frequency (buoyancy frequency, N^2), and the seasonal mixed layer depth (m). Seasonal mixed layer depth estimates were based on a change in density criterion of $\Delta\sigma_\theta$=0.03 kg m^{-3}, relative to 10 dbar (de Boyer Montégut et al. 2004).

A biological variable, the integrated estimate of water column chlorophyll-*a* (mg m^{-2}) was obtained using High Performance Liquid Chromatography (Wright et al. 2010, Westwood & Pearce 2018). Values for each station were integrated using a trapezoidal rule; i.e. stations where chlorophyll was present at the deepest depth sampled, 0 mg chlorophyll-*a* m^{-3} was assumed to occur 30 m deeper for integration purposes.

Two final environmental variables examined were the position of the sun and the time since sea-ice melt. The position of the sun (solar elevation, in degrees) relevant to the horizon (i.e., positive values=day-time, negative values=twilight to night-time) was calculated using the "maptools" (Bivand et al. 2018) package in R (R-Core-Team 2018). The time since sea-ice melt (weeks) was calculated from daily passive microwave estimates of sea-ice concentration (%), obtained from the National Snow and Ice Data Center SMMR-SSM/I 25 km resolution polar product available for the Southern Hemisphere (Cavalieri et al. 1996, updated yearly, Maslanik & Stroeve 1999, updated daily).

Statistical methods: Generalised Additive Models

Generalised Additive Models (GAMs, Wood 2006) with a log-link function were used to determine environmental variables associated with high KAXIS *S. thompsoni* abundances. GAMS are an analysis method regularly used to identify non-linear relationships between zooplankton populations and environmental conditions (Zarauz et al. 2007, Flores et al. 2012b, Kvile et al. 2016). Prior to modelling, all trawl locations were classified into three, broad oceanographic zones (based on the frontal locations shown by Bestley et al. (2018)): South of the SB, between the SB and the SACCF or north of the SACCF. These zones were treated as categorical variables. Oceanic zone was included as a discrete variable to consider the influence of circulatory parameters including sea-surface height: a feature that varies across ACC fronts (Sokolov & Rintoul 2009). A thin-plate smoothing spline (Wood 2003) was applied to each of the continuous environmental variables: weeks since sea-ice retreat, chlorophyll-*a* (mg m^{-2}), solar elevation (degrees), seasonal mixed layer depth (m), temperature minimum (°C) and buoyancy frequency (N^2). The continuous environmental variables were tested for

collinearity (Zuur et al. 2010) using Variance Inflation Factors. To identify which of the correlated variables was the best predictor of *S. thompsoni* distribution patterns, a series of GAMs that modelled KAXIS *S. thompsoni* abundances against oceanographic zone, chlorophyll-*a*, solar elevation and a single correlated variable was compared. All GAMs were fit using the R package "mgcv" (Wood 2011).

2.5 Results

Distribution patterns and life-stage of Salpa thompsoni*: routine and target trawls*

Approximately 80,000 *S. thompsoni* were sampled during routine RMT8 trawls, with an average density of 310 individuals (ind.) 1,000 m^{-3} (Table 2.1.). Aggregate *S. thompsoni* comprised 90% of the total catch, and solitaries comprised 10%. A group of high *S. thompsoni* abundances occurred at routine trawls 12, 13, 14 and 15, crossing the Princess Elizabeth Trough and both the SB and the SACCF (Fig. 2.2). For this group of trawls, abundances exceeded 1,500 ind. 1,000 m^{-3}, with a maximum of 2,560 ind. 1,000 m^{-3} at trawl 12. *Salpa thompsoni* was also collected during the trawl closest to the continent (trawl 0, near 93°E), but in low densities (10 ind. 1,000 m^{-3}). *Salpa thompsoni* and *Ihlea racovitzai* (the other Southern Ocean salp species) were both present in two trawls (21 and 34), but *I. racovitzai* was not present in any other routine RMT8 trawls. *Salpa thompsoni* was absent from three routine trawls at 60°S (25, 35, 37) and four between 63-65°S (1, 16, 19, 20); otherwise it was present in 33 out of 40 (82.5%) routine trawls.

Approximately 13,000 *S. thompsoni* were sampled during target trawls aimed at *E. superba* (Fig. 2.3.). Distribution patterns and life-stage composition of *S. thompsoni*

followed similar trends to the routine trawls: samples were dominated by *S. thompsoni* aggregates, with highest average abundances between the SACCF and the SB, and lowest average abundances found north of the SACCF. The highest abundance (2,670 ind. 1,000 m^{-3}) was in trawl 12 and, again in line with the routine sampling, *S. thompsoni* was absent from some trawls at 60 °S (three trawls), and between 63 °S–65 °S (four trawls). *Ihlea racovitzai* was absent from all target trawls.

Table 2.1 Summaries of 2016 *Salpa thompsoni* abundance data[a]

	Routine trawls		Target trawls	
Latitudinal extent (°S)	57.61, 65.46		58.23, 65.17	
Longitudinal extent (°E)	73.31, 93.59		72.65, 93.56	
Maximum sampled abundance (ind. 1,000 m^{-3})	2,560		2,670	
Av. abundance north of SACCF (ind. 1,000 m^{-3})	240		11	
Av. abundance between SACCF and SB	470		500	
Av. abundance south of SB (ind. 1,000m^{-3})	270		120	
Life stage	S	A	S	A
% compositions	10	90	1	99
Estimated total count)	(8,004)	(72,032)	(134)	(13,190)

[a]S, solitary; A, aggregate.

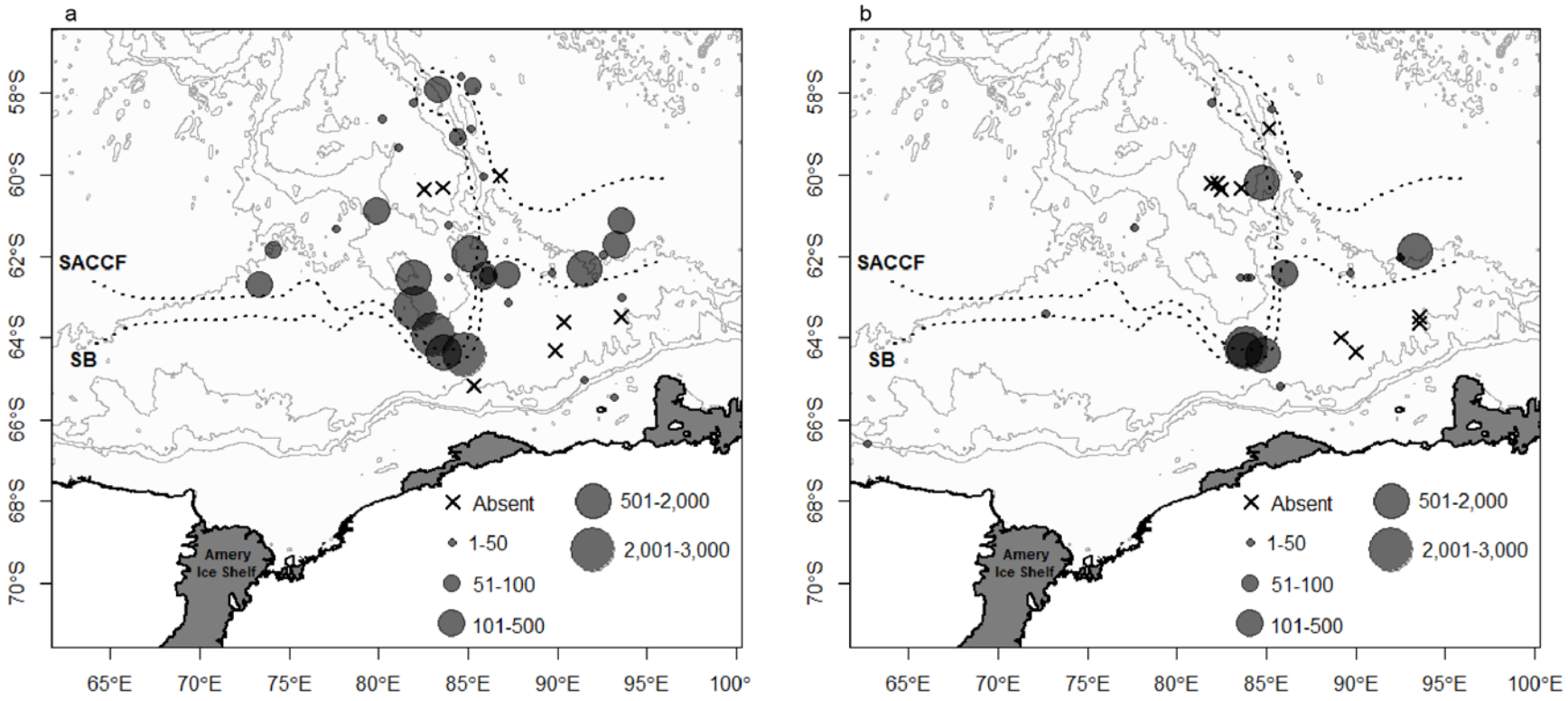


Figure 2.2 Routine (a) and target (b) RMT8 *Salpa thompsoni* densities (ind. 1,000 m^{-3}). Dotted lines show location of Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the Antarctic Circumpolar Current (SB), calculated from *in-situ* data (Bestley et al. 2018). Light grey lines show 500 m isobath

Population composition

Length-frequency data for aggregate and solitary maturity stages are presented in Figs. 2.3a and b, respectively. Within the *S. thompsoni* subsample (~1% of total sample) selected for morphometrics and life history data, all maturity stages for solitaries and aggregates were present. Of the aggregate subsample (n=764), 52% were developing, 26% were immature and 22% were mature individuals. The solitary subsample (n=55) comprised 44% developing, 33% immature and 24% mature individuals. The average aggregate oral-atrial length (OAL) was 20 mm, and the maximum OAL was 95 mm. For solitaries, the average OAL was 37 mm, with a maximum OAL of 84 mm.

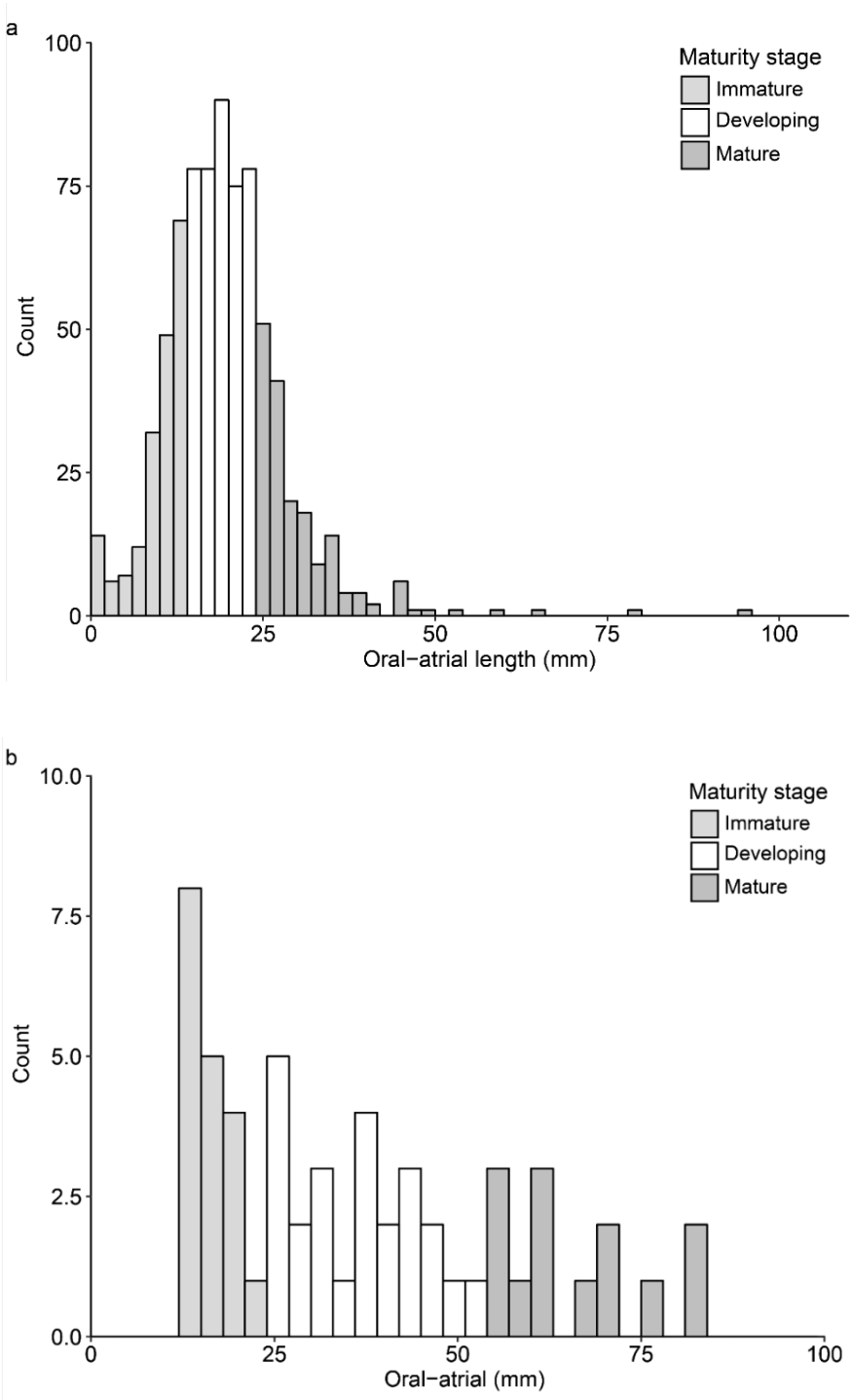


Figure 2.3a-b. Oral-atrial length vs number of individuals, by maturity stage, for (a) aggregate and (b) solitary *Salpa thompsoni*. Aggregate data are shown in 2 mm bins, and, to ensure visual clarity with fewer data points, solitary data are shown in 3 mm bins.

Fig. 2.4 compares the distribution of gut diameter, OAL and total length (TL) for aggregate and solitary length-maturity stages. For aggregates, the average TL of immature individuals was 21 mm (range = 2–54 mm), increasing to 23 mm (range = 23–65 mm) in developing individuals, and 55 mm (range = 28–111 mm) in mature individuals. The average TL of solitaries approximately doubled with maturity stage, increasing from an average of 21 mm (range = 15–34 mm) in immature individuals, to 42 mm (range = 29–65 mm) in developing individuals, and 73 mm (range = 62–97 mm) in mature individuals. Across both aggregates and solitaries, the largest difference between the OAL and TL was observed in developing aggregates, with the OAL comprising, on average, only 48% of the TL. In immature and mature aggregates, the OAL comprised, on average ~57% of the TL. The OAL of solitary salps comprised 83% of TL in immature individuals, 88% of the TL in developing individuals, and 91% of the TL in mature individuals.

Across both aggregates and solitaries, the average gut diameter more than doubled from immature to mature individuals. The gut diameter of solitaries increased uniformly (x 1.8) from immature (av.=5 mm, range=3–6 mm), to developing (av.=9 mm, range=5–15 mm), and mature (av.=16 mm, range=9–19 mm) individuals. On average, the gut diameter of aggregates was smaller than that of solitaries, however, the maximum gut diameters observed across the two life stages were similar. In aggregates, the average gut diameter doubled from immature (av.=4 mm, range=1–9 mm), developing (av.=8 mm, range=4–19 mm) individuals. From developing to mature aggregates, however, the average diameter increased to only 11 mm, and the range (5–20 mm) in mature individuals was almost identical to that of developing individuals.

Although average gut diameter increased across maturity stages, the overlap between the ranges of measurements for each stage reflects the large variation in salp gut size.

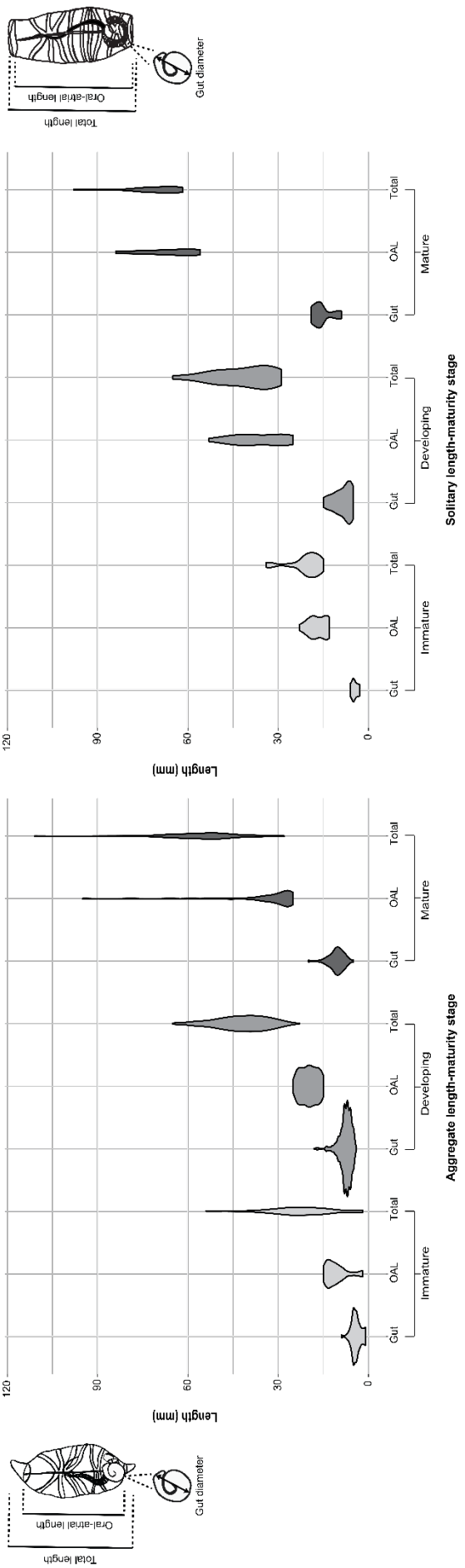


Figure 2.4 Distribution of gut, oral-atrial (OAL) and total length measurements, across three life stages of aggregate and solitary *S. thompsoni*. The widths of the plot markers are scaled according to the number of counts in each 1 mm bin, for the corresponding morphometrics parameter, i.e. the wider the marker, the more observations in that bin.

Historical comparison of routine trawl Salpa thompsoni *densities in the Kerguelen Plateau region*

Of the available historical *S. thompsoni* abundance data within the broader south Kerguelen Plateau area (58 °S–70 °S, 70 °E–105 °E), the sampling regions of the SIBEX II and AAMBER had the most overlap with the KAXIS sampling region (Figs. 2.5a-d). During SIBEX II and AAMBER, average *S. thompsoni* densities were 45 and 17 ind. 1,000 m^{-3}, respectively. Maximum *S. thompsoni* densities were 603 and 179 ind. 1,000m^{-3}, respectively, and were sampled between 60 °S and 63 °S. During the KAXIS voyage, highest densities were sampled further south, between 62 °S and 65 °S, with the largest bloom of the routine RMT8 trawls (2,560 ind. 1,000 m^{-3}) more than triple the SIBEX II and AAMBER maxima. The two most northern sites sampled during AAMBER II, situated in the narrow stream between the SACCF and the SB, overlap with the group of high KAXIS abundances, however, during AAMBER II, *S. thompsoni* were absent from this northern area. South of 64 °S, *S. thompsoni* were, historically, absent or present in low densities (<10 ind. 1,000 m^{-3}). Notably, the region immediately north of the Amery Ice Shelf was sampled during SIBEX II, AAMBER, AAMBER II, KROCK and BROKE, and, during these surveys, was typified by the lack of *S. thompsoni*. The BROKE and BROKE-West surveys overlap with the eastern and western borders of the KAXIS region, respectively. During BROKE-West, *S. thompsoni* were absent east of 70 °E, including along the 80 °E transect bordering the group of high KAXIS *S. thompsoni* densities. During BROKE, *S. thompsoni* were present in low densities west of 105 °E (average = 3 ind. 1,000 m^{-3}).

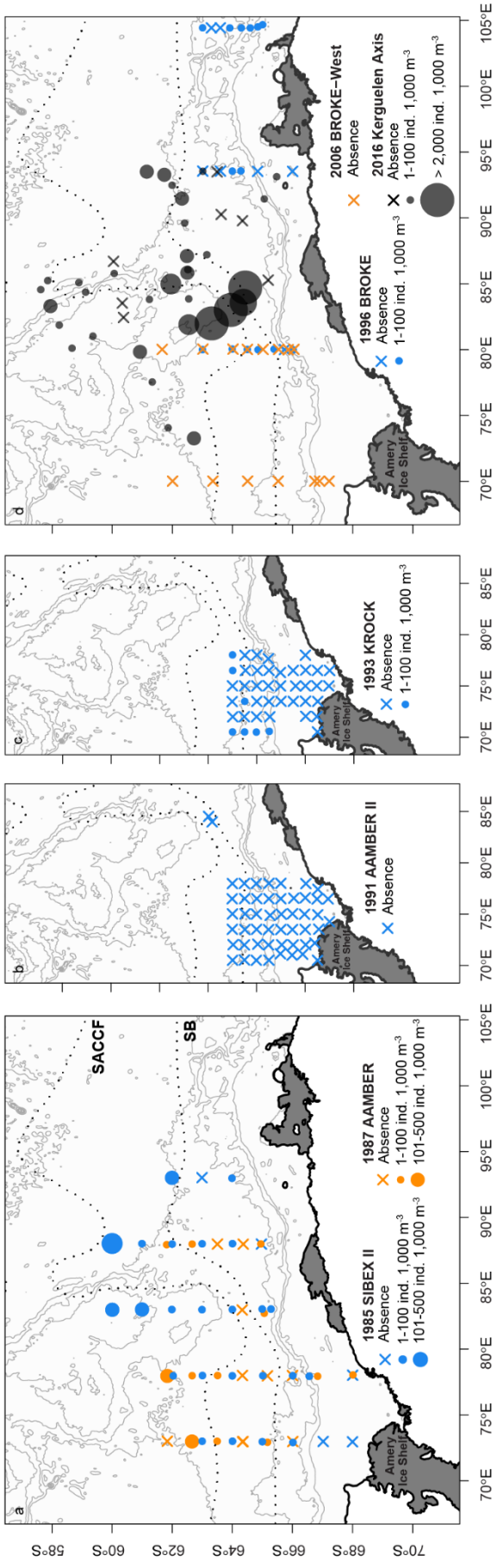


Figure 2.5a-d Summer *Salpa thompsoni* densities in the broader Kerguelen Plateau region: routine RMT trawls from 1985-2016. Dotted black lines show climatological location of the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SB) (Orsi et al. 1995). Light grey lines show 500 m isobaths. For visual clarity, trawls are separated into SIBEX II and AAMBER (a), AAMBER II (b), KROCK (c), and BROKE, BROKE-West and the Kerguelen Axis (d).

1992-2016 summer Salpa thompsoni densities in the broader Kerguelen Plateau region, under varying meridional sea-ice extent and SST conditions

Over twenty-five years, the average northern latitude of the winter sea-ice edge ranged between 57.31 °S during 2001 and 59.720 °S during 1995 (Fig. 2.6). No large-scale, long-term (1979-2010) change in seasonality has been identified in East Antarctic sea-ice (Massom et al. 2013) and, in this study, a Mann-Kendall test (Mann 1945, Kendall 1955) did not identify a significant linear, long-term trend in winter meridional sea-ice extent (Fig. A1.1, Table A1.4). In addition, no statistically significant linear, long-term trend was identified in 1992-2016 summer SST (Fig. A1.2, Table A1.5), which (from the ice-edge to 58 °S) ranged between -0.471 °C (2000) and 0.503 °C (1993). *Salpa thompsoni* were absent (KROCK and BROKE-West) during periods of high meridional winter sea-ice extent (58.07 °S, KROCK; 58.06 °S, BROKE-West), and both medium summer SST (0.136 °C, BROKE-West), and high summer SST (0.503 °C, KROCK) (Fig. 2.6). During BROKE, low *S. thompsoni* densities (average=3 ind. 1,000 m^{-3}) coincided with medium winter meridional sea-ice extent (58.41 °S) and low summer SST (-0.181 °C). The highest *S. thompsoni* abundances (average=310 ind. 1,000 m^{-3}), sampled during the KAXIS voyage, coincided with low summer SST (-0.130 °C) and low meridional winter sea-ice extent (59.22 °S) (Fig. 2.7).

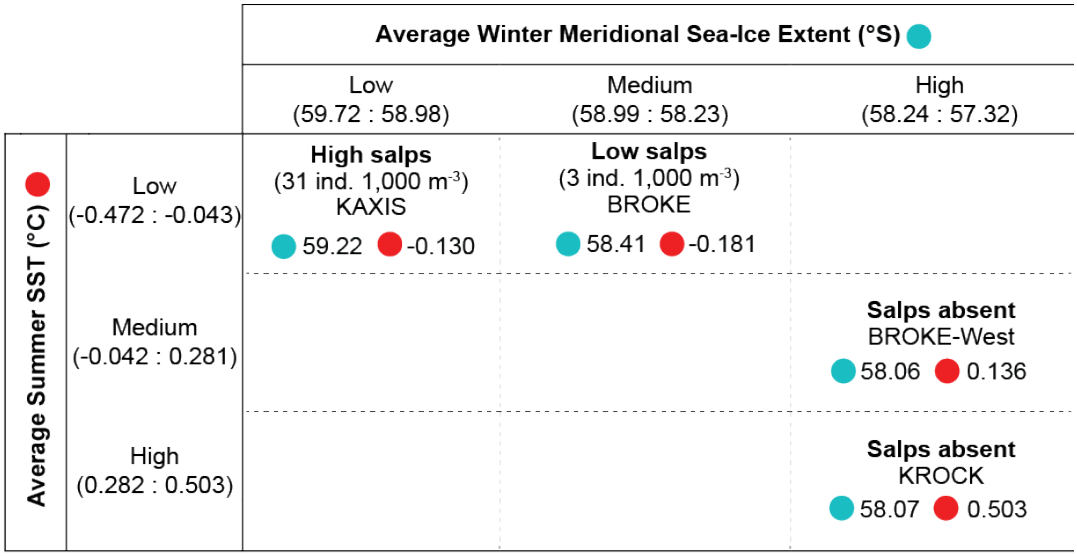


Figure 2.6 1992-2016 winter meridional sea-ice extent (blue dots), summer SST (red dots) and *Salpa thompsoni* densities for the region of 70 °E–105 °E. Low SST and winter meridional sea-ice extent, values below the 25th percentile; Medium, values between the 25th and 75th percentiles; High, values greater than the 75th percentile. Standard deviation of SST is 0.227 °C, and 0.540°S for maximum sea-ice extent. Blank spaces indicate that no sampling has occurred within the corresponding meridional sea-ice extent and SST conditions.

Environmental variables driving high Kerguelen Axis Salpa thompsoni *abundances: Generalised Additive Models*

Generalised additive models (GAMs) were used to identify environmental variables associated with the high KAXIS *S. thompsoni* abundances. Table 2.2 gives the results of the best fit GAM (based on greatest deviance explained, highest R-squared value and lowest Akaike Information Criterion). Collinearity of variables and other models are reported in Tables A2.6 and A2.7, respectively. In the most parsimonious model, the effects of oceanographic zone, weeks since sea-ice retreat and chlorophyll-*a* on *S. thompsoni* abundances were highly significant ($p<0.001$), and the effect of the sun's position was nonsignificant ($p=0.064$). Figs. 2.7a-7c show the relationship between *S. thompsoni* abundances and the smoothed variables, from the best fit GAM. Negative,

linear relationships were identified between *S. thompsoni* abundances and chlorophyll-*a* and the sun's position. These relationships associate higher *S. thompsoni* abundances in the top 200 m of the water column with lower chlorophyll-*a*, and solar elevation <0° (outside of peak daylight). A non-monotonic, nonlinear relationship was identified between *S. thompsoni* abundances and weeks since sea-ice retreat, suggesting that highest abundances occurred ~eight weeks since sea-ice presence.

Table 2.2 Best fit GAM for modelling environmental conditions to *Salpa thompsoni* Kerguelen Axis densities[a]

Model statistics		Model Terms				
Adj. R-sq.	Dev. exp.	Parametric Coefficients	Est.	St. Error	z-value	p-value
0.608	51.5%	South of SB	2.445	0.685	3.569	< 0.001
		Between SB and SACCF	6.136	0.562	10.921	< 0.001
		North of SACCF	4.195	0.443	9.466	< 0.001
		Smooth terms		DF	Chi-Sq.	p-value
		Time since ice retreat (weeks)		4.00	19.580	0.001
		Chlorophyll-*a* (mg m^{-2})		1.00	10.855	0.001
		Solar elevation (°fh)		1.00	3.434	0.064

[a]Adj. R-sq, adjusted R-squared value, DF, degrees of freedom; Est., estimated effect of variable on temperature; St. Error, standard error; °fh, degrees from horizon.

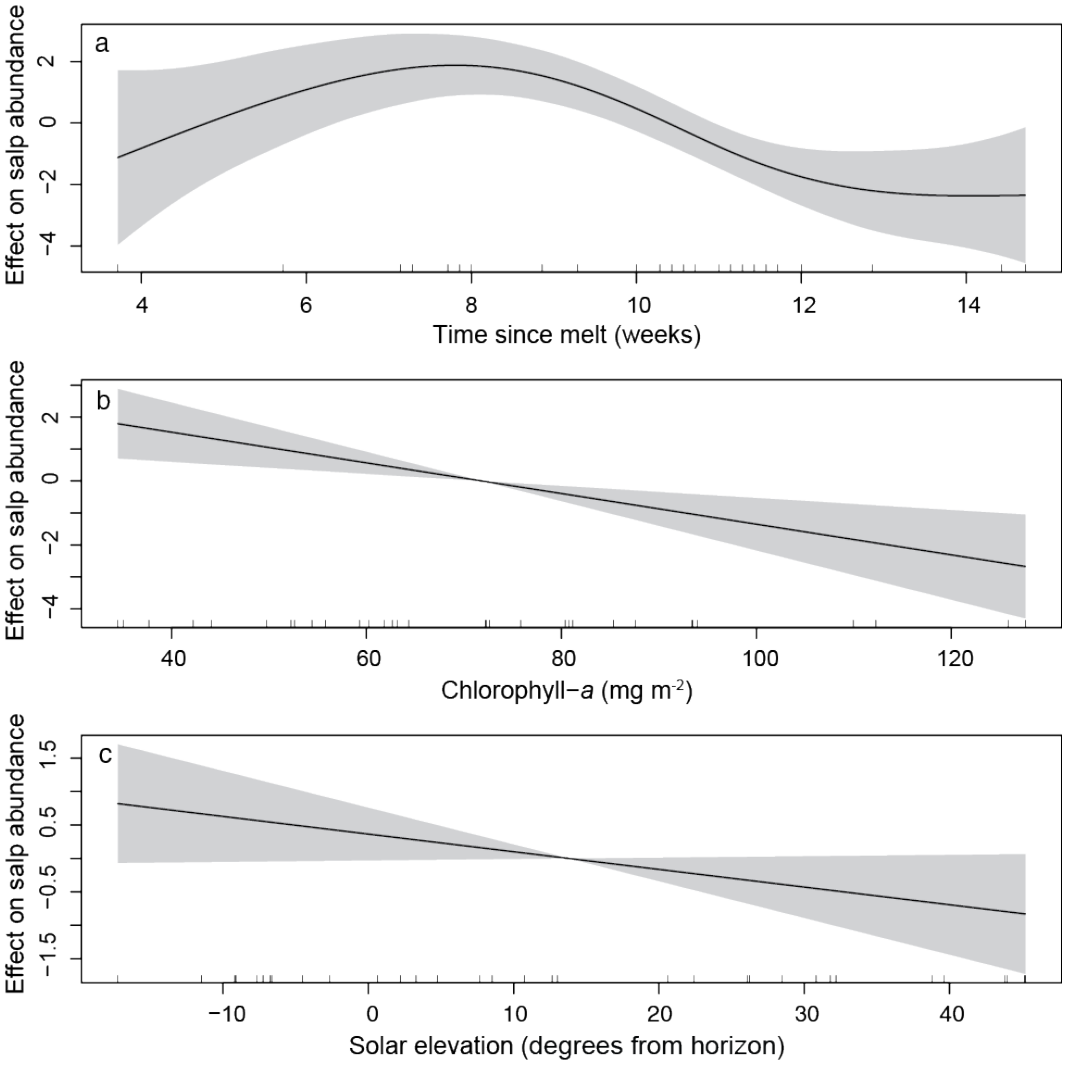


Figure 2.7a-c Generalised Additive Models of *Salpa thompsoni* densities. Effect of additive smooth functions of time since ice retreat (a), chlorophyll-*a* (b), solar elevation (c). Grey shaded area shows 95% confidence intervals of smoothers. Dashes along the x-axis, within the plotting area, are data points.

2.6 Discussion and conclusions

During January and February 2016, *S. thompsoni* blooms were a spatially persistent feature of the southern Kerguelen Plateau zooplankton community, and were sampled at thirty-three of forty routine trawl locations. The average *S. thompsoni*

density was over 300 individuals 1,000 m^{-3}, with the maximum bloom (sampled between 82-85°E in the narrow waters between the SACCF and the SB of the ACC) estimated at over 2,500 ind. 1,000 m^{-3}. Furthermore, the KAXIS maximum abundance exceeded the maxima recorded in the region during historical surveys by more than 4-fold (Hosie et al. 2000, Nicol et al. 2000b, unpublished historical data used in this study).

An examination of long-term environmental data showed *S. thompsoni* to be most abundant in the Indian Sector of the Southern Ocean during summers that follow low winter meridional sea-ice extent, while Generalised Additive Models linked high 2016 densities to open water at around eight weeks post sea-ice retreat conditions. These results may lead to the conclusion that, as has been shown in the waters off the West Antarctic Peninsula (Atkinson et al. 2004, Ross et al. 2014, Steinberg et al. 2015), decreased sea-ice presence is a key driver of *S. thompsoni* blooms in the Kerguelen Plateau region. The relationship between *S. thompsoni* and a lower northern sea-ice edge is consistent with the BROKE survey, where increased meridional sea-ice extent and high euphausiid abundances were present between 80 °E–115 °E, while decreased meridional sea-ice extent and high *S. thompsoni* abundances were present between 115 °E–150 °E (Nicol et al. 2000b).

The apparent surge in KAXIS *S. thompsoni* productivity following sea-ice retreat may be due to a shift in the phytoplankton community. Upon initial spring melt off the WAP, diatom blooms dominate the phytoplankton community. Melting sea-ice and glacial run-off, however, continue to reduce surface water salinity, and drive a shift towards a flagellate-based phytoplankton assemblage (Kang et al. 2001, Montes-Hugo et al. 2009), and a food community that, based on particle size, is favourable for *S.*

thompsoni. The link to sea-ice identified in this study is also in line with several West Antarctic studies (Siegel & Loeb 1995, Loeb et al. 1997, Atkinson et al. 2004), although Loeb et al. (2010) noted that the sea-ice hypothesis is best supported by the West Antarctic data series prior to 2003. The data collected prior to 2003 encompass frequent El Niño events and extremely reduced meridional sea-ice extent off the West Antarctic Peninsula. Since 2003, high West Antarctic *S. thompsoni* abundances have continued to be observed in low sea-ice conditions, however, more recent studies have found blooms to be best explained by the Southern Annular Mode and the multivariate El Niño Southern Oscillation Index (Loeb & Santora 2012, Steinberg et al. 2015). While the historical East Antarctic data used in this study data were sparse, the sampling regimes did cover multiple ENSO phases. The 1985 SIBEX II and 1996 BROKE occurred during La Niña summers; 1987 AAMBER, 2006 BROKE-West and 2016 Kerguelen Axis occurred during El Niño summers; while 1991 AAMBER II and 1993 KROCK occurred during neutral summers. In addition, the historical *S. thompsoni* densities, when compared alongside historical SST and sea-ice (from 1992 onwards) encompassed "low", "medium" and "high" meridional sea-ice extent conditions. This further demonstrates that, while the *S. thompsoni* abundance dataset was limited, it did not bias towards particular large-scale climatological conditions.

When attributing *S. thompsoni* distribution patterns to a discrete climatological or sea-ice parameter, region-specific relationships between ENSO and sea-ice ought to be considered. In the West Antarctic, sea-ice is lost through basal melt during an El Niño event (Paolo et al. 2018). In the East Antarctic, the relationship between El Niño conditions and sea-ice is less clear. The effect of El Niño periods (associated with warming in the eastern tropical Pacific) on sea-ice extent in the Indian Sector of the

Southern Ocean varies with season: inducing increased sea-ice area during summer, and a dipole-like pattern of anomalies during the winter (Deb et al. 2014). In this region, sea-ice area has continuously declined during El Niño Modoki events (to date, Modoki events have only been associated with warming in the central tropical Pacific, and cooling in eastern and western tropical Pacific) (Deb et al. 2014). The 2014-2016 El Niño event, coinciding with the KAXIS voyage, possessed Modoki-type elements (Huo & Xiao 2016). This poses the question of whether this relatively recently described climate phenomenon (Ashok & Yamagata 2009) is a major driver of *S. thompsoni* abundance, and possibly other gelatinous species, in the Indian Sector of the Southern Ocean. This study focused on *in-situ* environmental parameters and their relationship with *S. thompsoni*. However, future studies incorporating measurements of El Niño Modoki events may provide new information on the influence of this climatic mode on Southern Ocean salps and clarify basin-scale ENSO, and more localised sea-ice, effects.

In addition to sea-ice influences, the GAMs presented evidence of higher *S. thompsoni* abundances occurring in low chlorophyll-*a* waters. The inverse relationship between *S. thompsoni* and chlorophyll-*a* further supports findings from the 1996 BROKE survey. During BROKE, chlorophyll-*a*, as well as sea-ice extent, were together found to delineate the east/west sampling sectors: the western euphausiid-abundant waters were characterised by higher chlorophyll-*a*, whereas the eastern salp-dominated waters were a region of low primary productivity (Hosie et al. 2000). While *S. thompsoni* abundances from BROKE (Hosie et al. 2000) and BROKE-West (Swadling et al. 2010) were not modelled against a daylight variable, the effect of solar elevation identified in this study is consistent with the diel vertical migratory (DVM) behaviour expected for the species. During summer, *S. thompsoni* begins migrating from below the photic zone

around midday. From here, the species remains between 30–120 m depth until complete darkness, when it then moves to the surface (Nishikawa & Tsuda 2001). Diel vertical migration in zooplanktors is often attributed to predator avoidance (Zaret & Suffern 1976, Ringelberg 2009, Cohen & Forward Jr 2016), however, Nishikawa and Tsuda (2001) suggest DVM in *S. thompsoni* as a possible adaptation to oligotrophic environments, allowing for increased utilisation of food throughout the water column and, in turn, greater survivability in low-productivity waters. Based on previous DVM observations, *S. thompsoni* would have likely been in KAXIS routine trawl depth range (top 200 m of the water column) for the majority of afternoon and evening trawls. However, as the species has been observed at depths greater than 1,000 m (Pakhomov et al. 2011), it seems reasonable that any trawls prior to the commencement of DVM would likely underestimate population estimates. This knowledge of DVM in *S. thompsoni*, combined with the significance of solar elevation identified in this study, highlights the importance of evening/twilight sampling to obtain accurate Southern Ocean *S. thompsoni* densities.

The new information presented in this study provides preliminary answers to previously open questions surrounding what conditions comprise *S. thompsoni*-favourable habitat in the Indian Sector of the Southern Ocean. However, for a more complete understanding of the relationship between *S. thompsoni* and the East Antarctic environment, information is needed on the physiological responses of *S. thompsoni* to physical and chemical parameters. Pakhomov et al. (2002) highlighted the scarcity of circumpolar information on the feeding and ecophysiology of *S. thompsoni*, particularly south of 60°S. Over the past 15 years, only one study (Pakhomov et al. 2006) has thoroughly investigated this aspect of the species, finding a combination of suitable

food source availability, and the ability to complete both the asexual and sexual life cycles, as ecophysiological determinants of *S. thompsoni* survival. The ACC is one environmental feature that delineates changes in food availability and life cycle success of *S. thompsoni*. In this study, highest *S. thompsoni* abundances were observed north of the SB (defined by the southerly extent of warmer Upper Circumpolar Deep Water, and demarcating the subpolar regions; (Orsi et al. 1995)). This is consistent with how key ecophysiological and feeding mechanisms influence distribution patterns. Populations of *S. thompsoni* are typically restricted to waters north of the SB, where they can feed on small cyanobacteria and nanoflagellates (phytoplankton <1.4 µm—smaller than *S. thompsoni* feeding mesh—can still satisfy *S. thompsoni* metabolically; Sutherland et al. 2010). In the cooler waters south of the SB, larger coccolithophores (>2 µm) are more prevalent (Trull et al. 2001), and elevated particle concentrations are regularly observed at the marginal ice zone (Pakhomov et al. 2003). These features of the food environment make most high Antarctic waters unsuitable for salps: as indiscriminate filter feeders with a small mesh size (1.4 µm), they cannot easily digest large diatoms and coccolithophores (Sutherland et al. 2010) or adjust their ingestion rates under elevated particle concentrations (Pakhomov et al. 2006).

Over recent decades, *S. thompsoni* has been sampled increasingly further south; a trend that, in the West Antarctic, is associated with ocean warming and decreased sea-ice extent (Pakhomov et al. 2002, Atkinson et al. 2004). While the 2016 KAXIS densities are higher than those previously sampled in the area, a southerly shift, or even reproductive success south of the SB, cannot be confirmed without a continuous sampling regime, covering summer months of aggregate production, through to autumn

months of solitary production. At present, life cycle completion has been observed in the high Antarctic, but only in irregular intrusions of warmer Circumpolar Deep Water (Pakhomov et al. 2011). Changing characteristics of the ACC may facilitate future southward expansion of *S. thompsoni* distribution, in particular an accelerated warming rate of ~0.2 °C per decade (1982-2012) observed along zonal bands of its northern flank (Armour et al. 2016). Changes in sea-ice may further expand *S. thompsoni* habitat because decreased sea-ice extent has been associated with a decline in the size spectrum of Southern Ocean phytoplankton in the West Antarctic Peninsula region (Moline et al. 2008).

A circumpolar account of *S. thompsoni* distribution patterns with balanced east-west information is far from complete, owing to a lack of East Antarctic observational data. By providing baseline information on *S. thompsoni* dynamics in an understudied region, this study provides key information previously missing from east-west comparisons. Compared to long-term (1993-2009) West Antarctic *S. thompsoni* densities (Loeb & Santora 2012), the maximum and average abundances sampled during the KAXIS voyage were less than a "high salp summer" (mean=702–1396, max=18,486 individuals 1,000 m^{-3}), but higher than most "low salp summers" (mean=19–41, max=660 individuals 1,000 m^{-3}). The life stage composition of the KAXIS community, comprising ~90% aggregates and ~10% solitaries, is consistent with the most recent West Antarctic life history information in Loeb & Santora (2012). The dominance of immature individuals within the solitary life phase, and the prevalence of developing/mature aggregates, also suggests that KAXIS sampling coincided with the beginnings of solitary production, consistent with the reproductive cycle documented by

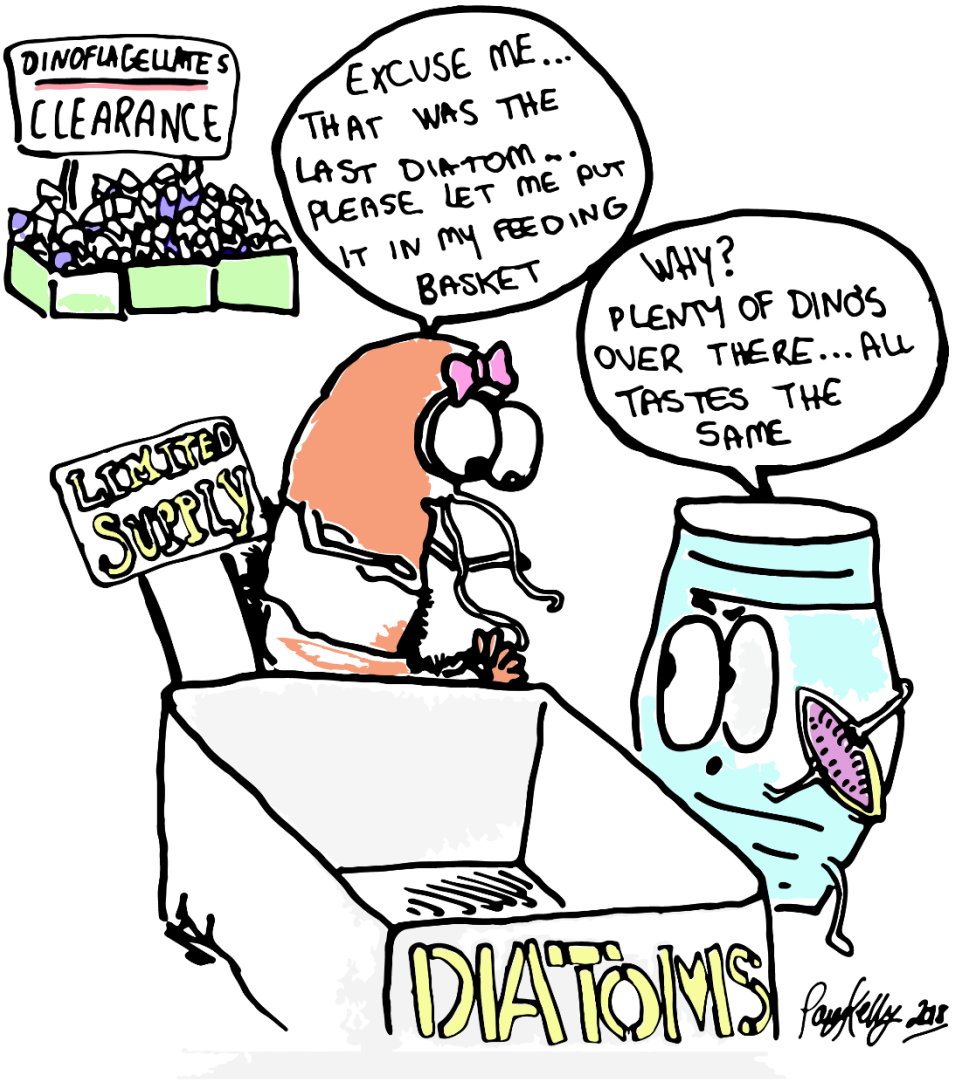
Loeb & Santora (2012). The steady decline in abundance from immature to mature solitaries is consistent with natural mortality, however, additional population dynamics might also have contributed to this trend. Such dynamics include an overlapment of generations due to individuals solitaries surviving for more than one year (as opposed to 7.5 months (Loeb & Santora 2012)), as well as there being a continuous (rather than pulsed) recruitment of solitary forms over the annual cycle.

The life-stage body length measurements documented here will also serve as baseline information for Indian Sector-specific models of salp growth rates (extending on the general model of Henschke et al. (2018), which estimates approximately 1 mm of growth d^{-1}). Furthermore, the morphometrics measurements in this Chapter bring to light potential complications when including *S. thompsoni* in size-based models or higher order predator energy budgets. In over 40% of subsampled KAXIS aggregate individuals, the total length was more than double the oral-atrial length. Due to the flexibility of *S. thompsoni* bodies, oral-atrial length is considered the standard length measurement, however, if being used to estimate biomass or nutritional value of an individual, or total space occupied by a *S. thompsoni* bloom, ultimate figures may be underestimated. I am not aware of any other published data on the *S. thompsoni* digestive system, preventing any direct comparisons across the literature. Gut diameter information in this study will aid future understanding of Indian Sector consumption capacity, and the species' overall grazing effect on phytoplankton biomass. In copepods, size metrics have proven particularly significant in estimating carbon ingestion rates (Valdés, Escribano & Vergara 2017), and for modelling ingestion rates as a function of predator capacity (Hansen, Bjørnsen & Hansen 1997). Furthermore, it is also speculated that the majority of the energetic content of *S. thompsoni* is derived from the gut (Gili et al. 2006), and increased

effort in reporting digestive metrics is required to quantify the energetic potential of *S. thompsoni*.

As well as complementing West Antarctic studies, the KAXIS *S. thompsoni* distribution information extends on previous work by Atkinson et al. (2004, 2016). which collated long-term *S. thompsoni* distribution patterns in the Indian Sector of the Southern Ocean, as part of a circumpolar analysis. Comparisons of Atkinson et al. (2004, 2016) with the current study highlight complexities in the analysis of *S. thompsoni* populations, including the importance of considering life history information when evaluating the ecological significance of statistical trends in abundances. In this study, historical RMT8 data collected from January-March showed the waters of the broader Kerguelen Plateau region to be an area of low *S. thompsoni* densities, with absences between 70 °E–80 °E. To the west of this study range, Atkinson et al. (2004) identified a long-term (1926-2003) density increase (greater than 2-fold per decade) in waters between 25 °E –45 °E. This trend is based on an increase in *S. thompsoni* from 0–2 individuals m^{-2}, to 4–8 individuals m^{-2}. Such low *S. thompsoni* abundances can be the result of advection rather than colonisation, and caution should be applied when attempting to translate a statistically significant trend in *S. thompsoni* populations into a trend that is ecologically significant. We apply similar restraint in interpreting the findings of the current study. While the maximum 2016 KAXIS densities were higher and occurred further south than historical sampling, comparable data in the broader region were temporally and spatially sparse. These limitations, in conjunction with the boom or bust nature of *S. thompsoni*, further highlight the need for additional sampling to confirm a long-term shift in distribution.

Additional data are needed to clarify the environmental drivers of increasing *S. thompsoni* abundances. Using data from the Kerguelen Plateau region (the limitations of which have been discussed), and through analysis methods appropriate for the available data, this study found sea-ice to be the most suitable predictor of *S. thompsoni* abundances. These results do not refute existing evidence of temperature-driven *S. thompsoni* abundances in the West Antarctic (e.g. Ross et al. 2014), or provide grounds for dismissing the potential effect of temperature in the Indian Sector. Instead, this study identifies environment-population relationships in a specific area of the Southern Ocean, at a specific point in time. Future sampling in the Indian Sector will improve understanding of the interplay between East Antarctic sea-ice, temperature and *S. thompsoni* abundances, and aid in refining region-specific hypotheses about the environmental drivers of salp blooms. Continued comparisons with West Antarctic studies will aid development of a circumpolar perspective. Even in light of the complexities that surround quantifying a bloom species, the abundance and life history information from this study will serve as a platform for future studies on salps in the Indian Sector of the Southern Ocean. Lines of research to be explored include the potential for habitat/food resource overlap between *E. superba* and *S. thompsoni*, and the potential of *S. thompsoni* as an alternative prey item for *E. superba* predators.


DINOFLAGELLATES
CLEARANCE
EXCUSE ME... THAT WAS THE LAST DIATOM... PLEASE LET ME PUT IT IN MY FEEDING BASKET
WHY? PLENTY OF DINO'S OVER THERE... ALL TASTES THE SAME
LIMITED SUPPLY
DIATOMS

CHAPTER 3

Resource overlap between *Salpa thompsoni* and *Euphausia superba* in the Kerguelen Plateau region of the Southern Ocean

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Preface:

Previous studies suggest that the Southern Ocean ecosystem is experiencing an increase in Salpa thompsoni (salps), coinciding with a decline in Euphausia superba. S. thompsoni is regularly referred to as a competitor of E. superba (Suprenand & Ainsworth 2017), however, the extent of resource overlap between the two species is unclear, particularly in the waters off East Antarctica. In this study, summer populations of E. superba and S. thompsoni were sampled in the Kerguelen Plateau region, in the Southern Ocean Indian Sector. Co-occurrences of E. superba and S. thompsoni within a 10 m depth range suggested small-scale spatial competition between these two species, while gut content analysis suggested additional competition for food. Compared to E. superba, S. thompsoni consumed a broader size range of phytoplankton, including Fragillariopsis diatoms typically consumed by E. superba. Based on stable isotope analysis of $\delta^{13}C$ *and* $\delta^{15}N$*, resource overlap between Indian Sector S. thompsoni and E. superba was greater than overlap between S. thompsoni and other Southern Ocean euphausiids. This new information on resource partitioning between Indian Sector S. thompsoni and E. superba will serve as a platform for future regional assessments of the changing ecosystem input, and subsequent effect on energy flow, from key zooplanktors.*

3.1 Highlights

- In the Kerguelen Plateau Region, 2016 *S. thompsoni* and *E. superba* populations overlapped on both horizontal (latitudinal and longitudinal) and vertical (water-column) spatial scales. Furthermore, this overlap was greater than that documented for Indian Sector regions in the past.
- Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ revealed the trophic position and diet of 2016 Kerguelen Plateau *E. superba* to be more like that of *S. thompsoni* than other euphausiids (*Euphausia frigida*, *Euphausia triacantha* and *Thysanoessa macrura*).
- Based on gut content analysis, Kerguelen Plateau *S. thompsoni* and *E. superba* do feed on the same key prey sources, primarily *Fragilariopsis* diatoms.
- *S. thompsoni* 'bycatch' in trawls targeting *E. superba* is prevalent in East Antarctic scientific sampling, and provides a unique opportunity to investigate interactions between *S. thompsoni* blooms and *E. superba* swarms.

3.2 Key words

Salpa thompsoni, *Euphausia superba*, Kerguelen Plateau, resource overlap, krill/salp interactions, stable isotope analysis.

3.3 Introduction

In the Antarctic and Southern Ocean, *Euphausia superba* is a major dietary component for fish, squid, whales, seals and penguins. Consequently, *E. superba* provide an essential ecosystem pathway for the transfer of nutrients, and energy, from phytoplankton to higher trophic levels (Murphy et al. 2007). Due to this pivotal role in energy transfer, the population dynamics of *E. superba* (i.e. seasonality, recruitment success, abundance, and distribution patterns) are major determinants of the current

structure and function of the Antarctic and Southern Ocean ecosystem (Murphy et al. 2013). Potentially compromising this *E. superba* energy pathway are recent climatic changes including warming ocean temperatures and a 40+ year low in sea-ice extent (Stuecker et al. 2017). In a warmer Southern Ocean, with less sea-ice, ecosystem-input from *E. superba* is expected to decrease (Flores et al. 2012a, Piñones & Fedorov 2016), while input from gelatinous species, such as the tunicate *Salpa thompsoni*, is expected to increase (Suprenand & Ainsworth 2017).

The concept of a sea-ice driven "see-saw" between West Antarctic *S. thompsoni* and *E. superba* was first presented by Siegel and Loeb (1995) and Loeb et al. (1997). In support of this hypothesis, Atkinson et al. (2004) then attributed a possible long-term decrease in West Antarctic *E. superba*, and long-term increase in *S. thompsoni*, to declining winter sea-ice extent. A number of more recent studies continue to present evidence of sea-ice driven West Antarctic *S. thompsoni*/*E. superba* co-dominance patterns, however, temperature, primary productivity and high-impact climate events are also identified as environmental influencers (Lee et al. 2010, Steinberg et al. 2015). Furthermore, recent findings highlight the spatial sensitivity in *S. thompsoni* population/environment relationships, with a cyclic abundance pattern observed in the near ice-free northern West Antarctic Peninsula (WAP), and an increasing abundance trend observed in the more ice-abundant southern WAP (Steinberg et al. 2015).

Compared to the West Antarctic, information on East Antarctic *S. thompsoni* populations, particularly those in the Indian Sector of the Southern Ocean, is limited. Broad-scale *S. thompsoni* distribution patterns in the Indian Sector were last explored during the 1996 BROKE (Baseline Research on Oceanography, Krill and the Environment) survey (Nicol et al. 2000a), with increased abundances associated with eastern waters

(115 °E–150 °E) of lower chlorophyll-*a*, warmer temperatures and decreased sea-ice extent (Hosie et al. 2000, Nicol et al. 2000b). In addition, smaller-scale studies have identified East Antarctic *S. thompsoni* blooms south of the Southern Antarctic Circumpolar Current Front (Hunt et al. 2007, Ono & Moteki 2013, 2017), a region traditionally considered (exclusively) *E. superba* habitat (Mackey et al. 2012). While uncertainty surrounds the ability of *S. thompsoni* to reproduce at these higher latitudes (Ono & Moteki 2013), the occurrence of such southerly East Antarctic *S. thompsoni* blooms emphasises the need for studies to improve existing knowledge of what environmental conditions permit a "low *S. thompsoni*/high *E. superba*" or "high *S. thompsoni*/low *E. superba*" summer, and to investigate both the potential for *S. thompsoni* and *E. superba* to co-exist and the extent of resource overlap when co-existence occurs.

Using existing knowledge of *S. thompsoni* and *E. superba* biology, feeding and distribution patterns, we can speculate about the potential for resource competition between the two species. Concerning feeding mechanisms, both *E. superba* and *S. thompsoni* are filter feeders. *E. superba* most efficiently ingest particles larger than 10-µm equivalent spherical diameter (McClatchie & Boyd 1983, Boyd et al. 1984, Ishii et al. 1986), and therefore prefer to feed on diatoms such as *Fragilariopsis* spp. (Atkinson et al. 2002, Schmidt & Atkinson 2016). Although large diatoms are *E. superba's* staple food, the species does exhibit flexible feeding behaviour and can alter their diet according to season (Meyer et al. 2010). On the other hand, salps, in general, have a preference for small prey; feeding efficiently on, and maintaining metabolic satisfaction from, particles between ~1 µm and 3 µm (Sutherland et al. 2010). Despite this preference for small particles, salps are able to ingest diatoms, including Southern Ocean *Fragilariopsis* and

Thalassiosira species (von Harbou 2013). Therefore, *S. thompsoni* and *E. superba* can compete for the same food sources, potentially resulting in less available prey items for *E. superba* consumption.

While the feeding behaviours of *S. thompsoni* and *E. superba* suggest potential prey overlap, the extent of this competition is also dependent on *S. thompsoni* and *E. superba* habitat crossover. Traditionally, *S. thompsoni* has been considered a sub-Antarctic (45°S–55°S) species (Foxton 1966), occurring north of the colder, high latitude waters preferred by *E. superba*. Recent studies, however, document *S. thompsoni* blooms south of lower-latitude Antarctic waters; a finding which suggests the potential for spatial overlap between *S. thompsoni* and *E. superba* populations. Complicating habitat overlap estimates is the potential for vertical segregation of the two species. Both adult *E. superba* and *S. thompsoni* undergo vertical migration (Nishikawa & Tsuda 2001, Tarling & Johnson 2006), potentially utilising a 500+ m depth range over a 24-hour period. Diel vertical migration may therefore serve as a passive avoidance method. In addition, there is evidence that, to reduce competition amongst euphausiids, *E. superba* and other Southern Ocean krill species including *Euphausia crystallorophias* and *Thysanoessa macrura,* partake in active habitat partitioning (Marrari et al. 2011). If *E. superba* or other Southern Ocean krill species alter such habitat partitioning behaviour to avoid *S. thompsoni*, then increasing salp blooms may result in a restructure of Southern Ocean krill vertical distribution. Habitat overlap is a particularly complex aspect of *S. thompsoni* and *E. superba* resource partitioning, and, to achieve an adequate understanding of *S. thompsoni*'s competitive measure, vertical overlap of individuals within the water column, as well as latitudinal/longitudinal overlap in distributions, must be resolved.

This study provides information essential for identifying the ecosystem role of *S. thompsoni* in an understudied region of the Southern Ocean; specifically with respect to distinguishing where habitat overlap occurs in 3D space and to characterising competition for prey between the two species. Using a combination of historical and contemporary data collected in the waters off East Antarctica, this chapter addresses these underexplored aspects of *S. thompsoni*/*E. superba* dynamics by answering the following questions:

1. In the waters off East Antarctica, where is the greatest potential for *S. thompsoni*/*E. superba* habitat overlap?

2. Under occurrences of East Antarctic co-existence, what phytoplankton species may be a common food source for *S. thompsoni* and *E. superba*?

3. Is resource overlap between *S. thompsoni* and Southern Ocean euphausiids evident across all krill species in the region, or confined to specific species (such as *E. superba*)?

3.4 Methods

*2016 Kerguelen axis (KAXIS) sampling locations (*Salpa thompsoni *and euphausiiids) and field methods*

During January-February 2016, the KAXIS marine science voyage sampled the zooplankton community at 40 locations (excluding unsuccessfully deployed or retrieved trawls) across the southern Kerguelen Plateau (between 73.31 °E and 93.50 °E), in the Indian Sector of the Southern Ocean (Fig. 3.1). The voyage track crossed the Southern Boundary of the Antarctic Circumpolar Current (SB) and the Southern Antarctic Circumpolar Current Front (SACCF), with trawl locations concentrated in the region of

the sea-ice edge near the Princess Elizabeth Trough and Southern BANZARE Bank, between 70 °E and 91 °E. *S. thompsoni* were collected using an RMT8 net (Baker et al. 1973), with a mouth diameter of 8 m^2, and a 4.5 mm mesh size. Net deployments were classified as either "routine" (pre-planned) or "target" (opportunistic). Routine trawls were oblique tows, providing an integrated sample from 200 m to near-surface. Routine trawl duration was 20-45 minutes, with each trawl covering an average horizontal distance of 1,200 m. Target trawls sampled approximately a 10-25 m depth range over 5-15 minutes duration. These were directed at an identified acoustic target (using the 38 and 120 KHz frequencies of calibrated Simrad EK60 scientific echo-sounders; Horten, Norway) suggesting the presence of a krill swarm.

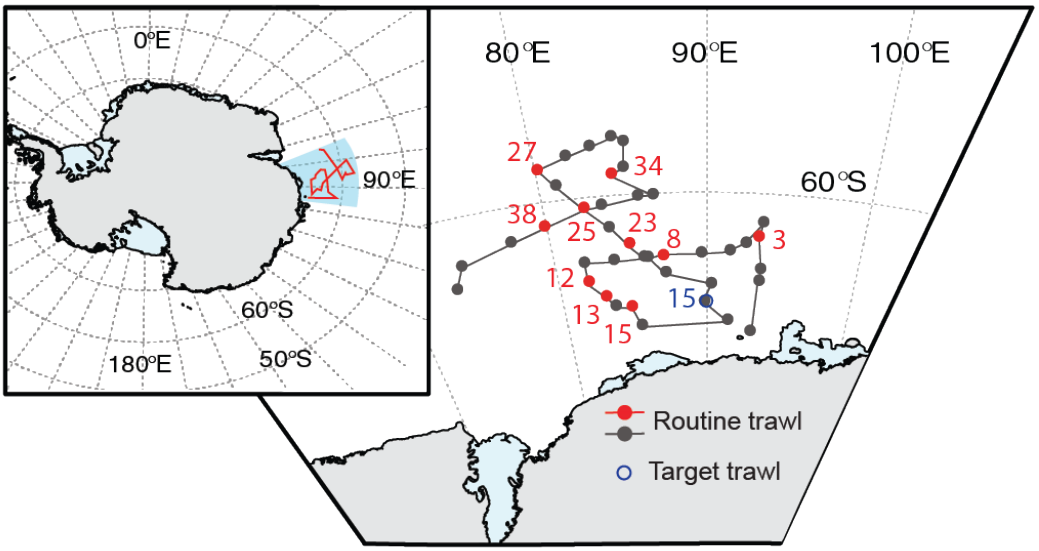


Figure 3.1 (left) Location of Kerguelen Axis study region (red trial on light blue background) with respect to the Antarctic continent and (right) Kerguelen Axis voyage track. Red circles connected by lines denote the location of routine trawl *Salpa thompsoni* and *Euphausia superba* used for stable isotope analysis, and the blue ring at station 15 denotes the location of the target trawl of salps and krill used for gut content analysis. The remainder of the routine trawls (grey circles connected by lines) are shown for visualisation of voyage track.

Kerguelen axis gut content analysis[1]

At target trawl 15 (89.99 °E, 60.34 °S), a subsample of twenty-five *S. thompsoni* and twenty-five *E. superba* were preserved in 4% buffered formaldehyde for gut content analysis. Prior to *E. superba* gut dissection, total body length (mm), digestive gland width (mm), sex, life stage and gut volume (cylindrical, ml) were recorded. The *E. superba* mid-gut was used for prey analysis to ensure consistency across individuals, and to avoid the influence of mechanical cell digestion by the gastric mill (McClatchie & Boyd 1983). Prior to *S. thompsoni* gut dissection, total length (mm), oral-atrial length (mm) and stomach volume (ellipsoidal; ml) were recorded. Whole *S. thompsoni* guts were extracted for analysis. After extraction, individual *E. superba* and *S. thompsoni* guts were split between two glass slides and macerated using a pinhead in a drop of MilliQ water. Due to the high concentration of cells in the *S. thompsoni* guts, 0.05% sodium carbonate solution was added to each slide to prevent clumping of particles.

Each slide was analysed under a Nikon DS-Ri2 light microscope (60x magnification) and five images taken (using the NIS-Elements BR (4.30.00) program). Randomly selected quadrats were overlaid on each image, and at least 100 cells identified across the quadrats. ImageJ (1.50i) was used to identify diatom species and estimate average surface area for each species (using the Global Diatom Database (Leblanc et al. 2012) as reference material). Cell surface area (averaged across up to twenty individuals for each diatom species), was used as a proxy for cell size. Cell sizes smaller than 3 μm were not considered in this study because of the difficulty in identifying small phytoplankton using a light microscope. It was estimated that 80% of items in *E. superba* guts were

[1] Gut content analysis was performed, and Fig. 3.5. produced, by Abigail Smith (ACE CRC/Institute for Marine and Antarctic Studies PhD candidate) as part of a 2016 undergraduate research research project.

large enough to be identified, and 30% of items in *S. thompsoni* guts were large enough to be identified.

Stable Isotope Analysis (SIA)

δ^{15}N can be used to estimate an organism's trophic position, with an increase between 1‰ and 5‰ (‰ is parts per thousand) typically distinguishing predator from prey (Minagawa & Wada 1984, Vander Zanden & Rasmussen 1999, Post 2002). δ^{13}C is used to identify food sources. Compared to δ^{15}N, it shows much weaker trophic enrichment, increasing from prey to predator by approximately 0.4 ‰ (Post 2002), maintaining the signature of the material of origin.

POM (Particulate Organic Matter): Particulate organic matter was sampled at ten locations (A3.1). Particles were retrieved by filtering water from the underway seawater line (5 m depth, maximum 300 L) at a pressure of 1.5 atm, through a 1 mm mesh (47 mm diameter). Once zooplankton were removed by passing through the 1 mm mesh, water samples were then filtered through 210 μm Nitex mesh and 1.2 μm Sterlitech silver filters, yielding particulate organic matter between 1.2 and 210 μm, and 210 and 1,000 μm. δ^{13}C and δ^{15}N of the two size classes were determined via in-line combustion continuous flow Isotope Ratio Mass Spectroscopy at Australian Nuclear Science and Technology Organisation. Samples were combusted using a Thermo Fisher Flash 2000HT Elemental Analyser, and the gases transferred to a Thermo Fisher Delta V plus IRMS through a Thermo Fisher Conflo IV. Estimates are relative to IAEA secondary certified standards, with an estimated analytical standard error (1 standard deviation) of ±0.3 ‰.

***Salpa thompsoni* and euphausiids:** *S. thompsoni* and euphausiids were collected for stable isotope analysis at nine routine trawl stations (Table 3.1). Samples were

immediately frozen in liquid nitrogen, and stored at -80°C. To prepare samples for SIA, salps and krill were thawed, rinsed with MilliQ water, and oven dried at 60°C to constant mass (between 24-48 hours as drying time was dependent on size). Dried contents were ground to a fine powder and 0.3–0.9 mg extracted for analysis. Stable isotope analysis and elemental composition (C, N) were determined via an Isoprime100 Elemental Analyser, in NCS combustion mode. δ^{13}C and δ^{15}N estimates (expressed as δ values in parts per 1,000 (‰)) were relative to Pee Dee Belemnite and atmospheric nitrogen, respectively (using the international reference standards USGS 24, 40 and 41, NBS 21), and were based on the equation:

$$\delta X=[(R_{sample}/R_{standard})-1]x1000$$

Where δX is δ^{13}C or δ^{15}N, and R is the ratio of ^{13}C/^{12}C or ^{15}N/^{14}N.

Systematic errors for nitrogen and carbon were estimated at 0.02‰ and 0.09‰, respectively.

Lipids were not removed prior to analysis, rather reported δ^{13}C values were corrected for lipids. Krill species were corrected via a variant of Fry (2002), modified for euphausiids by Logan et al. (2008) and *S. thompsoni* were corrected via the aquatic animal equation of Post et al. (2007). For the SIA results of this study to be most compatible with the results of previous studies (e.g. Stowasser et al. 2012, Pinkerton et al. 2013), guts of *S. thompsoni* and the krill species were also not removed prior to analysis.

Table 3.1 2016 Kerguelen Axis routine trawls sampled for *S. thompsoni* and euphausiid stable isotope analysis.

KAXIS Trawl	Date/Time (UTC)	Latitude (°S)	Longitude (°E)	Species	n
R03	2016-01-24T07:44:31	61.718	93.327	*S. thompsoni*	9
R08	2016-01-27T07:44:28	62.470	87.158	*S. thompsoni* *E.superba* *T. macrura*	17 10 13
R12	2016-01-29T20:20:58	63.292	82.042	*S. thompsoni*	10
R13	2016-01-29T11:08:06	63.930	83.065	*S. thompsoni*	10
R15	2016-02-01T05:30:30	64.410	84.769	*S. thompsoni* *E. superba*	8 8
R23	2016-02-05T11:23:00	61.936	85.035	*S. thompsoni* *E. superba*	9 7
R25	2016-02-06T13:27:42	60.362	82.497	*E. superba* *E. frigida* *T. macrura*	2 12 10
R34	2016-02-10T16:21:14	59.101	84.411	S. thompsoni *E. frigida* *E. triacantha* *T. macrura*	10 12 10 7
R38	2016-02-13T15:03:58	60.910	79.882	*S. thompsoni* *E. frigida*	14 7

Historical Salpa thompsoni *and* Euphausia superba *routine trawl density data: 1984-2016*

To assess the potential for horizontal (latitudinal/longitudinal) habitat overlap between East Antarctic *S. thompsoni* and *E. superba* in the photic zone, historical (occurring prior to the 2016 KAXIS voyage) density (individuals 1,000 m^{-3}) data were collated for the region of 30 °E–160 °E. Data were only selected if samples were collected from late spring to early autumn by an oblique tow of approximately 200 m in length and using an RMT8 net. Data from the KAXIS voyage, as well as data from eleven

historical surveys (1984-2008, Table 3.2), were used, with estimates of horizontal habitat overlap derived from "routine trawls," and estimates of vertical overlap derived from "target trawls."

Table 3.2 1984-2016 routine trawls studies for horizontal *Salpa thompsoni*/*Euphausia superba* habitat overlap[a].

Survey	Date Range	Latitudinal Extent (°S)	Longitudinal Extent (°E)	Routine Trawls (n)	Max. Depth (m)
ADBEX2	20/01/1984	63	58	1	200
SIBEX2	04/01/1985	60 – 68	57.97 – 93	38	250
AAMBER1	07/03/1987-23/03/1987	61.82 – 68	62.97 – 87.98	25	215
AAMBER2	19/01/1991-14/02/1991	64.98 – 69	64.11 – 78	59	232
FISHOG	25/01/1992-11/02/1992	51.01 – 52.59	71.44 – 76.57	21	250
KROCK	15/01/1993-07/02/1993	64.99 – 69	59.99 – 78.03	78	200
BROKE	30/01/1996-22/03/1996	62.99 – 66.31	80 – 150.03	64	200
KACTAS	14/01/2001-21/01/2001	65.99 – 66.86	62.79 – 64.50	32	240
UM0405	06/01/2005-14/02/2005	62.91 – 67.75	34.5 – 140.13	12	200
BROKE-West	19/01/2006-27/02/2006	61.66 – 69.11	29.99 – 80.02	46	206
UM0708	28/01/2008-08/02/2008	61.99 – 66.36	139.82 – 143.31	16	200
KAXIS	22/01/2016-15/02/2016	57.61 – 65.46	73.31 – 93.59	40	200

[a]Historical data sources; ADBEX2, Hosie (1999, updated 2017a); SIBEX2, Hosie (1999, updated 2017c); AAMBER1, Hosie (1999, updated 2014b), AAMBER2, Hosie (1999, updated 2014a); FISHOG, Hosie and Nicol (2000, updated 2017)), 1993 KROCK (Hosie 1999, updated 2017b), 1996 BROKE (Hosie & Nicol 2000, updated 2017), 2001 KACTAS

(Kawaguchi et al. 2006), 2005 UM0405 (Ishimaru 2005), 2006 BROKEWEST (Swadling & Kawaguchi 2007, updated 2017), 2008 UM0708 (Ishimaru 2008).

Historical Salpa thompsoni *and* Euphausia superba *target trawl density data: 1984-2016*

To assess the potential for vertical overlap between East Antarctic *E. superba* and *S. thompsoni*, historical (occurring prior to the 2016 KAXIS voyage) density (individuals 1,000 m^{-3}) data were collated for the region of 30 °E–160 °E (Table 3.3). Data were selected if samples were collected during a summer/autumn target trawl using an RMT8 net, and the tow covered a vertical depth range of no greater than 10 m. Minimum *E. superba* swarm height is ~2–3 m (Klevjer et al. 2010, Tarling & Thorpe 2014), however, swarms regularly exceed this minimum and can reach 30–40 m in height (Tarling et al. 2009, Cox et al. 2010). It was assumed that nets trawling within the 10 m depth range sampled a discrete mass, and not separate layers of *E. superba* and *S. thompsoni*. Also, 10 m depth was the minimum variation in trawl depth that also included the majority of the data: most target trawls fished over at least a 5 m range, therefore only including trawls sampling 0–3 m depth variation would have reduced the dataset by over half.

Table 3.3 1981-2016 target trawls studied for vertical *Salpa thompsoni*/*Euphausia superba* habitat overlap[a].

Survey	Date Range	Lat. Extent (°S)	Lon. Extent (°E)	Trawls (n)	Depth Range (m)	Depths Fished (m)
FIBEX	17/02/1981-08/03/1981	64.17 – 67.4	63.98 – 85.85	21	4	10-17, 27-32, 38-42, 48-62, 73-87, 93-97, 108-127
ADBEX2	18/01/1984	66.23 – 66.24	61.76 – 61.80	2	5-8	79-87
SIBEX2	19/01/1985	61.02 – 64	77.94 – 77.96	2	1-8	12-20, 30

ADBEX3	11/10/1985	66.90	70.25	1	10	45-55
AAMBER1	09/03/1987-16/03/1987	63.76 – 66.9	70.25 – 78.01	3	1-6	15-20, 50-56, 130
FISHOG	20/02/1992-06/03/1991	63 – 68.37	70.18 – 80.39	23	1-10	8-10, 15-18, 20-25, 30-35, 38-55, 70-80, 120, 210
KROCK	16/01/1993-06/02/1993	65 – 67	61.5 – 77.66	17	1-10	5, 18, 20-35, 40-64
BROKE	30/01/1996-21/03/1996	62.99 – 66.32	80 – 150	61	1-10	6-89, 100, 117-124, 134-139, 195
MERTZ	07/08/1999	67.08 – 67.18	144.69 – 144.92	2	1	20, 30
KACTAS	16/01/2001-11/02/2001	63.75 – 66.74	63.65 – 105.49	8	1-10	10, 21-27, 40, 45, 50-55, 70-80, 74, 84
KAXIS	23/01/2016-19/02/2016	58.38 – 66.81	62.88 – 93.56	29	1-10	10-85, 130-145, 220

[a]Historical data sources (not already referenced in Table 3.2); FIBEX, (Hosie 1999, updated 2018); ADBEX3, (Hosie & Williams 1999, updated 2017); MERTZ, (Hosie 2000, updated 2017).

Data analysis and graphics

Graphic production and data analysis were completed in R version 3.5.0, using the packages Rgdal (Bivand et al. 2018), rworldmap (South 2011), graticule (Sumner 2016), raadtools (Sumner 2015), ggplot2 (Wickham 2016) and stats (R-Core-Team 2018) packages.

3.5 Results

Elemental composition and $\delta^{13}C$ and $\delta^{15}N$ of 2016 Salpa thompsoni*,* Euphausia superba*,* Euphausia frigida*,* Euphausia triacantha *and* Thysanoessa macrura *from the Kerguelen Plateau*

Carbon and nitrogen content (% dry body weight) was lowest, and most variable, in *S. thompsoni* (Fig. 3.2a, Table 3.4). For *S. thompsoni*, carbon content ranged from 6 to 40% (av.=18.4%) while nitrogen ranged from 1 to 9% (av.=3.6%). For reference, both percent and mg carbon and nitrogen per *S. thompsoni* and euphausiid individual are listed in A3.2. The average carbon and nitrogen content of euphausiids were at least double those of *S. thompsoni*. Average carbon content was highest in *T. macrura* (av.=49.8%, range=44-56%). Across euphausiids, the carbon content species trend was the inverse of the nitrogen content-species trend, with nitrogen highest in *E. frigida* (av.=10.3%, range=8-12%) and lowest in *T. macrura* (av.=8.2%, range=6-10%).

The $\delta^{13}C$ and $\delta^{15}N$ separated the POM, *S. thompsoni* and four euphausiid species into four trophic groups (Figure 3.2b, Table 3.4). The group with the lowest $\delta^{13}C$ and $\delta^{15}N$ comprised the >1.2-210 µm and >210-1,000 µm POM. The POM $\delta^{13}C$ and $\delta^{15}N$ did not significantly differ between the two size classes, however, the ratios of both size classes were significantly different from every other taxonomic classification (Tables 3.5, 3.6).

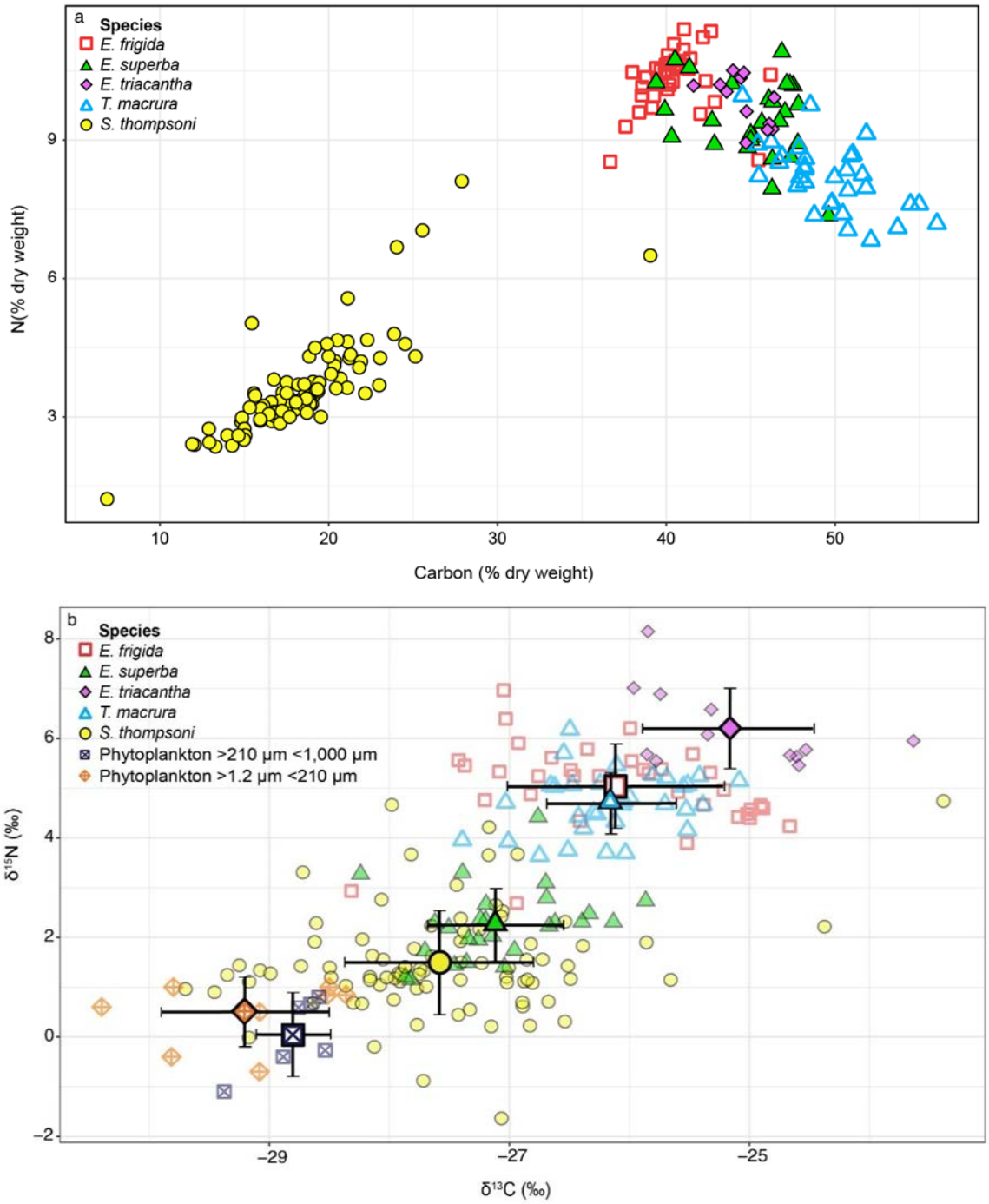
The group with $\delta^{13}C$ and $\delta^{15}N$ closest to those of particulate organic matter comprised *S. thompsoni* and *E. superba*. On average, $\delta^{13}C$ and $\delta^{15}N$ in *S. thompsoni* and *E. superba* were greater than POM $\delta^{13}C$ and $\delta^{15}N$ by at least one ‰. Of the seven taxonomic classifications, variation in $\delta^{13}C$ and $\delta^{15}N$ was greatest in *S. thompsoni*. Across *S. thompsoni*, $\delta^{13}C$ ranged between -23.38‰ and -29.70‰, and $\delta^{15}N$ between -1.64‰ and 4.74‰ (Figure 3.2b, Table 3.4). $\delta^{15}N$ of *S. thompsoni* and *E. superba* significantly differed from one another, however $\delta^{13}C$ did not (Tables 3.5, 3.6). In addition, both $\delta^{15}N$ and $\delta^{13}C$ of *S. thompsoni* and *E. superba* significantly differed from the remainder of the euphausiids and the POM.

The group with the third highest, and most similar, average $\delta^{13}C$ and $\delta^{15}N$ profiles consisted of *T. macrura* and *E. frigida* (Fig. 3.2b, Table 3.4). In addition, $\delta^{13}C$ and $\delta^{15}N$ of *T. macrura* and *E. frigida* were significantly different from the remainder of krill species and the POM (Tables 3.5., 3.6). The highest average $\delta^{13}C$ (-25.1 ± 0.74‰) and $\delta^{15}N$ (6.20 ± 0.81‰) values were observed in *E. triacantha*. Average $\delta^{13}C$ and $\delta^{15}N$ in *E. triacantha* were significantly different from the remainder of krill species and the POM.

Table 3.4 2016 KAXIS Salpa thompsoni and euphausiid stable isotope analysis[a].

Species	Average % C, (range)	Average % N, (range)	Average ‰ $\delta^{13}C$, (range)	Average ‰ $\delta^{15}N$, (range)
Salpa thompsoni	18.4 (6 – 40)	3.6 (1 – 9)	-27.58 ± 0.78 (-29.70 to -23.38)	1.5 ± 1.05 (-1.64 to 4.74)
Euphausia superba	44.7 (39 – 50)	9.5 (7 – 11)	-27.11 ± 0.56 (-28.24 to -25.86)	2.25 ± 0.73 (1.15 to 4.43)
Euphausia frigida	41.1 (36 – 47)	10.3 (8 – 12)	-26.11 ± 0.91 (-28.32 to -24.66)	5.04 ± 0.85 (2.69 to 6.97)
Euphausia triacantha	44.5 (41 – 47)	9.9 (8 – 11)	-25.16 ± 0.74 (-25.96 to -23.63)	6.20 ± 0.81 (5.46 to 8.15)
Thysanoessa macrura	49.8 (44 – 56)	8.2 (6 – 10)	-26.15 ± 0.74 (-27.39 to -25.08)	4.69 ± 0.61 (3.64 to 6.18)
POM (1.2 - 210 µm)			-29.2 ± 0.7 (-30.40 to -28.40)	0.5 ± 0.7 (-0.70 to -1)
POM (210 – 1,000 µm)			-28.8 ± 0.31 (-29.38 to -28.53)	0.05 ± 0.76 (-1.10 to 0.8)

[a]C, carbon; N, nitrogen.



Figures 3.2a-b (a) Carbon and nitrogen content (% dry weight) of KAXIS *Salpa thompsoni*, *Euphausia superba*, *Euphausia frigida*, *Euphausia triacantha* and *Thysanoessa macrura*, and (b) $\delta^{13}C$, $\delta^{15}N$ (‰ (per mil)) of KAXIS particulate organic matter, *Salpa thompsoni*, *Euphausia frigida*, *Euphausia triacantha* and *Thysanoessa macrura*. In figure b, small squares and circles in the plotting field are data points, and the larger squares and circles represent means. Error bars are standard deviation.

Table 3.5 Differences in $\delta^{13}C$ across taxa: One-way ANOVA results and Tukey's Honest Significance Difference Test[a,b]

ANOVA				
Source	MS	Df	F	P
$\delta^{13}C$ across all taxa	30.004	6	42.63	<.0001
Tukey's HSD Test				
Source	diff.	Lower bound	Upper bound	P
Small POM-large POM	-0.390	-1.740	0.960	0.978
S. thompsoni-small POM	1.616	0.693	2.538	<0.001
S. thompsoni-large POM	1.226	0.171	2.280	0.011
E. superba-small POM	2.086	1.080	3.092	<0.001
E. superba-large POM	1.696	0.568	2.823	<0.001
S. thompsoni-E. superba	-0.470	-1.020	0.079	0.148
T. macrura-S. thompsoni	1.433	0.917	1.949	<0.001
T. macrura-E. superba	0.962	0.309	1.615	<0.001
E. triacantha-S. thompsoni	2.439	1.660	3.198	<0.001
E. triacantha-E. superba	1.958	1.091	2.825	<0.001
S. thompsoni-E. frigida	-1.470	-1.969	-0.970	<0.001
E. superba-E. frigida	-0.999	-1.639	-0.359	<0.001
T. macrura-E. triacantha	-0.996	-1.842	-0.150	0.010
T. macrura-E. frigida	-0.037	-0.648	0.575	0.999
E. triacantha-E. frigida	0.959	0.123	1.795	0.013

[a]MS, mean square; df, degrees of freedom; F, F-value; P, P-value (significance is at the 0.05 level); diff, average difference between taxa.

[b]Post-hoc results compare taxa against others within the same trophic group, or those in neighbouring trophic groups.

Table 3.6 Differences in $\delta^{15}N$ across taxa: One-way ANOVA results and Tukey's Honest Significance Difference Test[a,b].

ANOVA				
Source	MS	Df	F	P-value
$\delta^{15}N15$ across taxa	112.61	6	142.8	<0.001
Tukey's HSD Test				
Source	Diff	Lower bound	Upper bound	P-value
Small POM-large POM	0.400	-1.028	1.83	0.981
S. thompsoni-small POM	1.046	0.070	2.023	0.027
S. thompsoni-large POM	1.446	0.330	2.562	0.003
E. superba-small POM	1.800	0.735	2.865	<0.001
E. superba-large POM	2.200	1.007	3.394	<0.001
S. thompsoni-E. superba	-0.754	-1.336	-0.173	0.003
T. macrura-S. thompsoni	3.198	2.652	3.744	<0.001
T. macrura-E. superba	2.444	1.753	3.135	<0.001
E. triacantha-S. thompsoni	4.707	3.894	5.521	<0.001
E. triacantha-E. superba	3.953	3.036	4.871	<0.001
S. thompsoni-E. frigida	-3.543	-4.072	-3.015	<0.001
E. superba-E. frigida	-2.789	-3.467	-2.111	<0.001
T. macrura-E. triacantha	-1.509	-2.404	-0.614	<0.001
T. macrura-E. frigida	-0.345	-0.992	0.302	0.690
E. triacantha-E. frigida	1.164	0.279	2.049	0.002

[a]MS, mean square; df, degrees of freedom; F, F-value; P, P-value (significance is at the 0.05 level); diff, average difference between taxa.

[b]Post-hoc results compare taxa against others within the same trophic group, and those in neighbouring trophic groups.

Across the approximate 35 years of routine trawl data, low *S. thompsoni* densities (0-100 ind. 1,000^{-3}) sampled alongside low *E. superba* densities (0-50 ind. 1,000 m^{-3}) was the most common co-occurrence combination, observed in 164 of the 200 1 ° x 1 ° cells analysed (Table A2.3). Medium *S. thompsoni* densities (101-1,000 ind. 1,000 m^{-3})

sampled alongside low *E. superba* densities was the second most common combination, observed in 23 cells. No cells were sites of high *S. thompsoni*/high *E. superba* density overlap.

The highest *E. superba* densities were sampled along 140 °E, as part of the UM0708 survey (Figs. 3.3a, b). During UM0708, the maximum average *E. superba* density across a 1x1° box was 385 ind. 1,000 m^{-3} (averaged from 65-66 °S, 139-140 °E), with 3,900 ind. 1,000 m^{-3} the maximum density sampled in a single trawl. Habitat overlap between *E. superba* and *S. thompsoni* was low across this (65-66 °S, 139-140 °E) box, with UM0708 trawls averaging 40 *S. thompsoni* ind. 1,000 m^{-3} . Higher salp densities were sampled along 140 °E during the 1996 BROKE survey (maximum 500 individuals 1,000 m^{-3} sampled in a single trawl), however, these were accompanied by very low *E. superba* densities (<10 ind. 1,000 m^{-3} sampled in a single trawl).

Another region of higher *E. superba*, but low *E.superba*/*S. thompsoni* habitat overlap, was that bordering the western edge of the Amery Ice Shelf. Here, the highest *E. superba* densities across a 1°x1° box were 140 ind. 1,000 m^{-3} (-67-68 °S, 69-70 °E), with a maximum of 430 ind. 1,000 m^{-3} sampled in a single trawl (AAMBER2 voyage, at -66.5 °S, 70.5 °E). Within the same box, *S. thompsoni* averaged 1 ind. 1,000 m^{-3}.

The most northern site of medium-high *E. superba* densities was 62.4 °S, 89.7 °S. Here, 317 individuals 1,000 m^{-3} were sampled in a single trawl. Only 1 *S. thompsoni* was sampled at this location, and this high *E. superba*/low *S. thompsoni* community composition was atypical compared to the density ratios observed at other northern sampling locations. In addition to the southern KAXIS survey region, medium-to-high *S. thompsoni* densities were consistently recorded in the northern KAXIS survey region,

and between 51 °S–52.59 °S, 71.4 °E–76.57 °E (sampled entirely during the FISHOG voyage). In the northern KAXIS region (57.6 °S–61.97 °S, 74.12 °E –93.56 °E), the maximum average number of *S. thompsoni* across a 1°x1° box was 584 ind. 1,000 m^{-3} (also the maximum number of *S. thompsoni* sampled during a single trawl, at 61.94 °S, 85.04 °E). For the region 51.00 °S–52.59 °S, the maximum average number of *S. thompsoni* across a 1°x1° box was 82 ind. 1,000 m^{-3}, with 274 ind. 1,000 m^{-3} the maximum sampled during a single trawl (at 51.27 °S, 72.99 °E). Unlike the southern half of the KAXIS stations, these northern regions of higher *S. thompsoni* densities were typified by little or no *E. superba* habitat overlap. *E. superba* was absent from the area (51 °S–52.59 °S, 71.4 °E–76.57 °E) and was present in low densities (maximum 37 ind. 1,000 m^{-3}) in 4 of 18 KAXIS north of 62 °S.

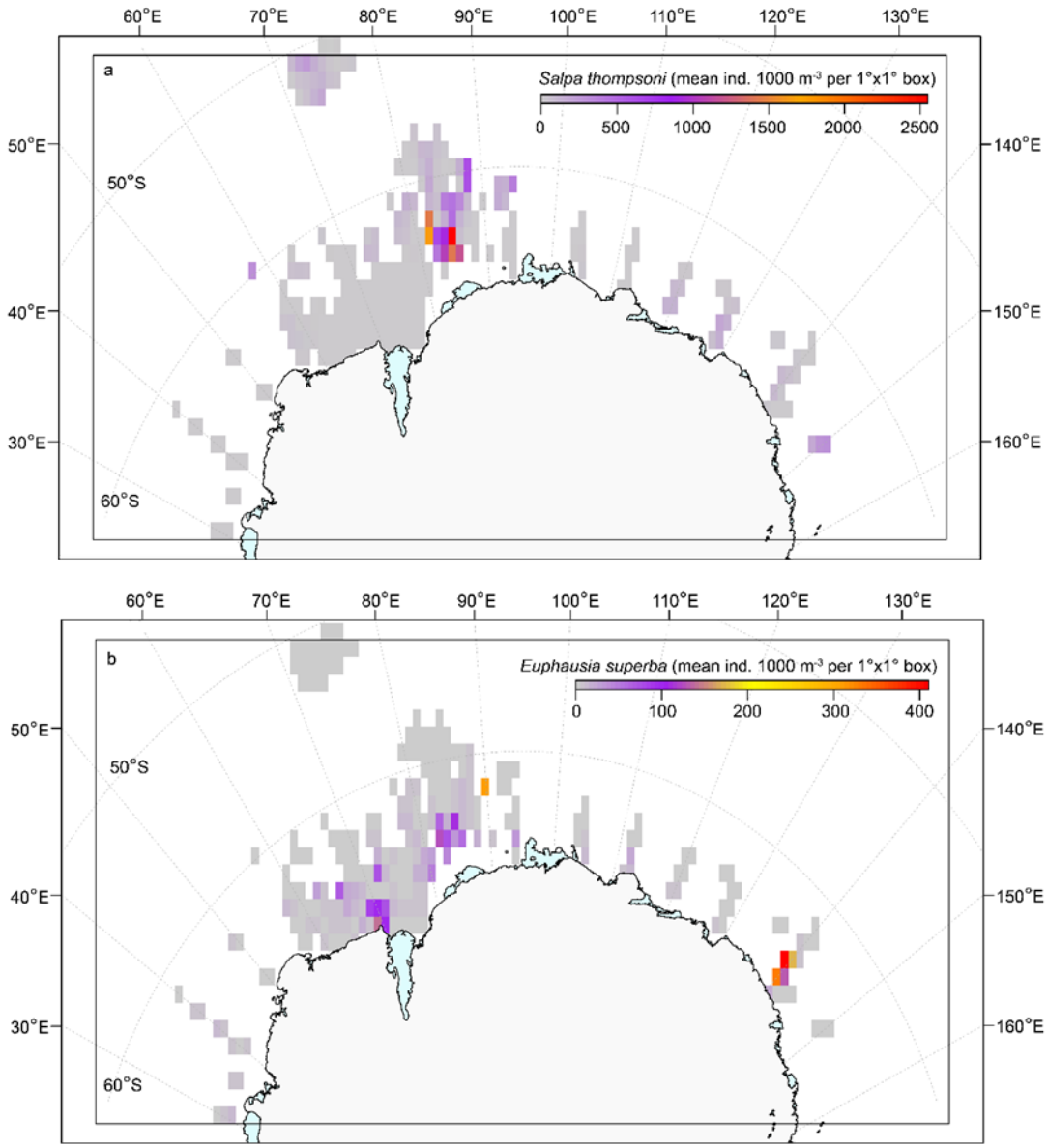


Figure 3.3 1984-2016 Indian Sector *Salpa thompsoni* (a) and *Euphausia superba* (b) densities (ind. 1,000 m^{-3}). Data are from routine trawls, and are averaged over a 1°x1° box. *Salpa thompsoni* and *E. superba* abundances are plotted on different scales for ease of visualisation.

Water column (10 m vertical depth range) habitat overlap between Salpa thompsoni *and* Euphausia superba*.*

From 1981-2016, during summer, narrow-depth target trawls were deployed in the region (58 °S–68 °S, 61 °E–150 °E), sampling the top 210 m of the water column (Fig. 3.4). Samples of 100% *E. superba* comprised 62% (90/146) of all narrow-depth trawls. With the exception of SIBEX II, all voyages returned at least one trawl comprising 100% *E. superba*. For the remainder of trawls, a mix of high (85-99%) *E. superba* and low (1-14%) *S. thompsoni* was most common, with this mix only absent from FISHOG and ADBEX II. This high *E. superba*/low *S. thompsoni* composition comprised 14% (20/146) of all narrow-depth trawls. A medium-high (50-84%) *E. superba* and low-medium (16-50%) *S. thompsoni* composition was less common, occurring across four voyages (FISHOG, BROKE, KACTAS and KAXIS), and accounting for 5% (8/146) of trawls. No narrow-depth target trawl returned a combination of medium-low (16-50%) *E. superba* and medium-high (50-85%) *S. thompsoni*. Three voyages (FISHOG, BROKE and KAXIS) returned trawls of low (1-15%) *E. superba* and high (85-99%) *S. thompsoni*, with these trawls also accounting for 5% (8/146) of total narrow-depth trawls. During KROCK, BROKE and KAXIS, some narrow-depth target trawls aimed at *E. superba* returned 100% *S. thompsoni* (Fig. 3.4). These 100% *S. thompsoni* samples comprised 14% (20/146) of total trawls—the same percentage of all trawls as those returning high *E. superba*/low *S. thompsoni*. While only one KROCK trawl returned 100% *S. thompsoni*, nearly one quarter of narrow-depth BROKE and KAXIS trawls (13/55 and 6/26 trawls, respectively) returned 100% *S. thompsoni*. Furthermore, BROKE and KAXIS were the only voyages where 100% *E. superba* trawls were less common than trawls returning a mix of *E. superba* and *S. thompsoni.*

Exclusive *E. superba* — Co-occurrences — Exclusive *S. thompsoni*

Cruise	Date range	Depth range (m)	Lat. extent (°S)	Lon. extent (°E)	Krill (%) 100	Krill (%) <100 ≥85 Salps (%) ≥1 <15	Krill (%) <85 ≥50 Salps (%) ≥15 <50	Krill (%) <50 ≥15 Salps (%) ≥50 <85	Krill (%) <15 ≥1 Salps (%) ≥85 <100	Salps (%) 100
FIBEX	17/02/1981-8/03/1981	10-127	64.17, 67.40	62.98, 85.85	16	2				
ADBEX II	18/01/1984	45-87	66.23, 66.24	61.76, 61.80	2					
SIBEX II	19/01/1985	12-30	64, 64.02	77.94, 77.96		2				
AAMBER I	9/03/1987-16/03/1987	15-130	63.76, 66.90	70.25, 78.01	1	2				
FISHOG	4/03/1992-6/03/1992	8-210	63.97, 67.87	70.18, 80.39	14		1		1	
KROCK	04/02/1993-01/02/1993	5-64	65, 67	61.53, 77.66	14	1				1
BROKE	24/02/1996-17/02/1996	6-195	62.99, 66.32	79.99, 150	26	7	4		5	13
KACTAS	16/01/2001-11/02/2001	10-84	63.75, 66.74	63.65, 105.49	5	2	1			
K-Axis	19/02/2016-9/02/2016	10-145	58.38, 66.81	62.88, 93.3	12	4	2		2	6

Figure 3.4 *Salpa thompsoni* and *Euphausia superba* composition, 1981-2016 narrow-depth (<10 m) target trawls aimed at *Euphausia superba*. Numbers within circles indicate the number of trawls from the respective voyage (labelled to the left) that comprised the *Salpa thompsoni*:*Euphausia superba* composition indicated above.

Food partitioning between Salpa thompsoni *and* Euphausia superba*: Gut content analysis*

Overall, thirty phytoplankton taxonomic groups were identified within the *S. thompsoni* and *E. superba* guts (Fig. 3.5). The taxonomic groups comprised twenty-six diatoms, two dinoflagellates (*Protoperidinium* sp. and *Dinophysis* sp.), one sillicoflagellate (*Stephanocha speculum*) and one chlorinated compound associated with cyanobacteria (*Trichotoxin* sp.). Each of the thirty taxonomic groups were present in at

least one *S. thompsoni* gut, while nineteen groups were present across *E. superba* mid-guts. Absent from all *E. superba* mid-guts were *Asteromphalus sp*., *Chaetoceros dichaeta*, *Chaetoceros* sp., *Corethron pennatum*, *Eucampia antarctica*, hexagonal centric diatoms, *Nitzschia* sp., *Rhizosolenia* sp., *Pseudo-nitzschia* sp., *Protoperidinium* sp. and small pennate diatoms. Across both *S. thompsoni* and *E. superba* guts, *Fragilariopsis kerguelensis* (*E. superba* av.=42 ind. gut^{-1}, *S. thompsoni* av.=32 ind. gut^{-1}) and *Fragilariopsis* sp. (*E. superba* av.=31 ind. gut^{-1}, *S. thompsoni* av.=37 ind. gut^{-1}) were present in the highest average abundances. The remainder of cells in *E. superba* mid-guts were mostly *Trichotoxin* sp. (av. = 30 ind. gut^{-1}) and small centric diatoms (av.= 16 ind. gut^{-1}). The remainder of cells in *S. thompsoni* guts were mostly the diatom *Thalassiothrix* sp. (av=20 ind. gut^{-1}), small pennate diatoms (av.= 11 ind. gut^{-1}) and *Fragilariopsis rhombica* (av.= 11 ind. gut^{-1}). All other phytoplankton groups consumed by *E. superba* and/or *S. thompsoni* were present in average abundances <10 individuals gut^{-1}.

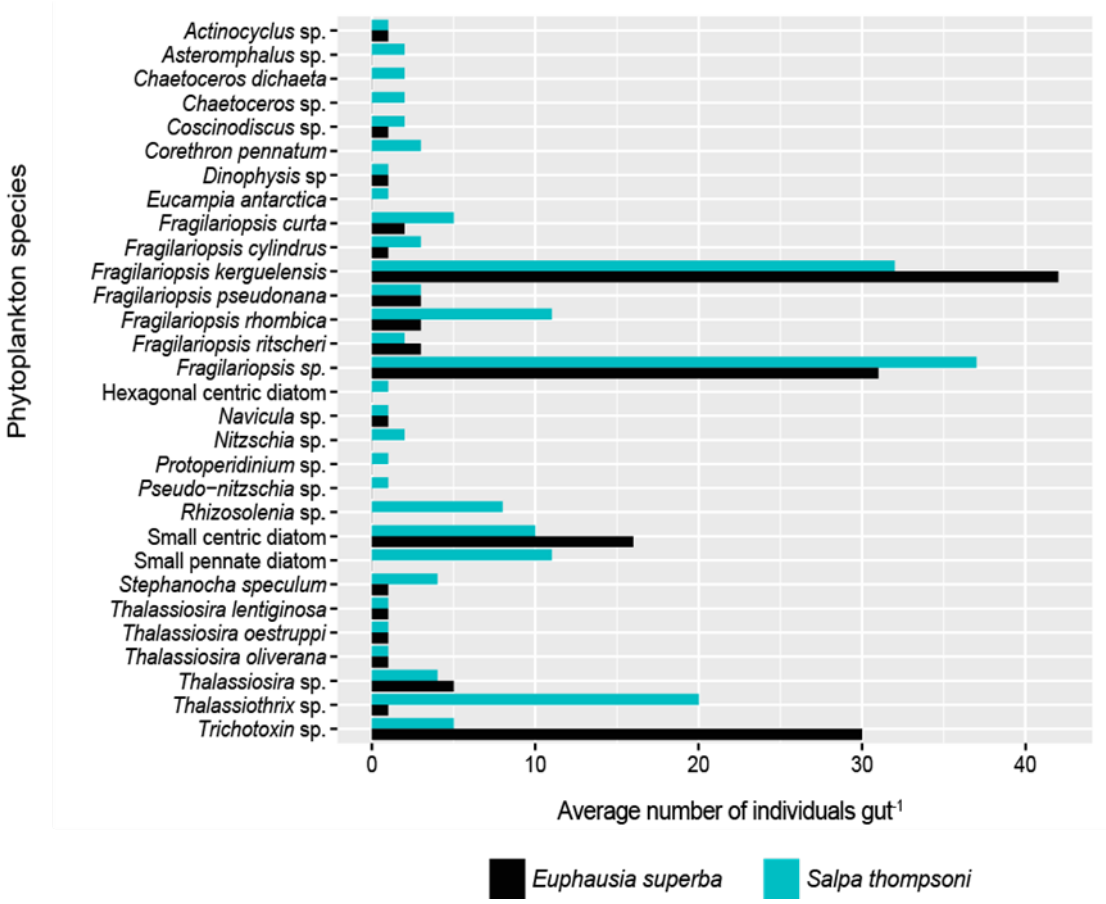


Figure 3.5 Phytoplankton taxa >3 µm, identified in KAXIS *Salpa thompsoni* (blue) and *Euphausia superba* (black) guts.

3.6 Discussion

Increasing *S. thompsoni* abundances may significantly alter future Southern Ocean food web structure, leading to changes in ecosystem structure that may alter the relative biomass of higher trophic levels. Resource overlap between *S. thompsoni* and *E. superba* is one pathway through which such changes may occur, however, information on this relationship is limited, particularly in the waters off East Antarctica. Findings from this study suggest that, in this region of the Southern Ocean, *S. thompsoni* has the potential to co-exist with *E. superba*, and compete with this keystone species for habitat and food.

Spatial overlap between KAXIS Salpa thompsoni *and* Euphausia superba

Based on routine trawl data from scientific surveys spanning 1984-2016, the southern Kerguelen Plateau (62 °S–66 °S, 82 °E–87 °E) is a region of *S. thompsoni* and *E. superba* horizontal and vertical habitat overlap. During January and February 2016, both species were sampled in 76% of routine trawls during the KAXIS voyage, with a highest broad-scale co-occurrence of 2,250 ind. 1,000 m^{-3} *S. thompsoni* and 605 ind. 1,000 m^{-3} *E. superba*. Potential broad-scale habitat overlap, albeit to a lesser degree, was also observed in the northern Kerguelen Plateau region in 2016, and, during 1996 and 2008, along the western edge of the Amery Ice Shelf, and the 140 °E line of longitude.

One of the key historical surveys in the Indian Sector, BROKE, found clear spatial segregation between *S. thompsoni* and *E. superba* populations, attributing an eastern *S. thompsoni* concentration to decreased chlorophyll-*a*, warmer temperatures and lower sea-ice extent, and a westerly *E. superba* concentration to higher chlorophyll-*a*, cooler temperatures and increased sea-ice extent (Hosie et al. 2000, Nicol et al. 2000b). During the subsequent BROKE-West survey, *S. thompsoni* was most abundant along the 30 °E line of longitude: the western-most edge of the sampling bounds. The BROKE-West mesoplankton community was surveyed with an RMT1 net (315 µm and mouth size of $1m^2$), which is too small to adequately sample *E. superba* adults (Swadling et al. 2010). Consequently, environment-abundance analyses of co-occurring BROKE-West *S. thompsoni* and *E. superba* are not available in the literature. Still, comparisons of RMT8 data in this study suggest that the BROKE-West survey region was an area of little or no broad-scale habitat overlap.

In the West-Antarctic, *S. thompsoni* and *E. superba* populations are, typically, spatially distinct (Pakhomov et al. 2002, Atkinson et al. 2004, Steinberg et al. 2015).

Peaks in West Antarctic krill and salp abundances may also be temporally discrete, with the zooplankton community "sea-sawing" between summers of krill and salp dominance (Ross et al. 2014, Steinberg et al. 2015). Still, some broad-scale habitat overlap has been observed off the West Antarctic Peninsula (Ross et al. 2008). Furthermore, in the waters off the southern WAP, there is evidence of increased positive anomalies in *S. thompsoni* abundances (Steinberg et al. 2015) occurring alongside a southerly shift in maximum *E. superba* densities (Ross et al. 2014). These co-occurring trends highlight the fact that *S. thompsoni*/*E. superba* population interactions may extend outside of direct habitat overlap, and further investigation is required to clarify whether, in conjunction with physical and chemical environmental change, *S. thompsoni* populations are driving a southerly shift in *E. superba* distributions. The effects of *S. thompsoni* blooms on the range extent of *E. superba* cannot be elucidated without improved understanding of bloom movements, and research methods that allow for more continuous collection of information than net hauls, e.g. unmanned aerial vehicles, may prove key in providing more detailed characterisations of aggregations (as they have for gelatinous species in temperate regions) (Schaub et al. 2018).

Horizontal overlap in *S. thompsoni* and *E. superba* populations at the Kerguelen Plateau during the 2016 summer was higher than that documented for Indian Sector regions in the past. While the temporal and spatial inconsistency of sampling within the Indian Sector makes it difficult to assess the true commonality of *S. thompsoni* and *E. superba* co-occurrences, this recent heightened horizontal habitat overlap warrants investigation into vertical habitat overlap in the Indian Sector. Both *E. superba* and *S. thompsoni* vertically migrate (Nishikawa & Tsuda 2001, Tarling & Johnson 2006), shifting their distribution between surface waters and the near-benthos for reasons including

predator avoidance and feeding. Through diel vertical migration, each species may actively avoid the other, and, subsequently, finer-scale habitat overlap within the water column cannot automatically be assumed from latitudinal/longitudinal habitat overlap. In this study, data from target trawls aimed at *E. superba* swarms, fishing within 10 m depth, were deemed most appropriate for estimating the potential for *E. superba* and *S. thompsoni* to occupy the same vertical space in the water column. While the majority of narrow depth target trawls retrieved 100% *E. superba*, one quarter of trawls sampled a mix of *S. thompsoni* and *E. superba* ("mixed trawls"), and 14% sampled all *S. thompsoni*. When trawls were mixed, it was most common for the trawl to comprise <15% *S. thompsoni*.

The target trawl compositions bring to light the potential for vertical overlap in *S. thompsoni*/*E. superba* to complicate sampling of *E. superba* swarms. *S. thompsoni* "bycatch" in historical (prior to 2016) *E. superba*-targeted trawls may have been due to persistent issues with acoustically identifying the two masses. When investigating the acoustic properties of salps, Wiebe et al. (2010) found that the backscattering of salp aggregate chains yielded a similar target strength (a measure of the reflection coefficient of a target) to that of *E. superba*, acknowledging the difficulty in differentiating *E. superba* swarms from *S. thompsoni*. In addition, Wiebe et al. (2010) noted that, during some trawls, a substantial number of *S. thompsoni* were retrieved when aiming for supposed *E. superba* swarms. More recent voyage observations (So Kawaguchi 2018, personal communication, November 12; Sven Gastauer 2018, personal communication, November 21), however, suggest that acoustic methods can adequately distinguish *E. superba* from *S. thompsoni*, and that retrieving mixed trawls is most likely due to populations of both species moving after net deployment. While the presence of

salps in target trawls aimed at *E. superba* may be a common nuisance for research voyages, these mixed target trawls do provide a unique opportunity to investigate interactions between *E. superba* swarms and *S. thompsoni* chains, and the potential for either species to avoid the other.

Ecologically, the occurrences of mixed *S. thompsoni*/*E. superba* target trawls suggests potential for vertical, photic zone habitat overlap across the Indian Sector. During the BROKE and BROKE-West surveys, depth-stratified sampling of the zooplankton community was not undertaken, however, more recently, the depth distribution of *S. thompsoni* off Adélie Land has been investigated. Along 140 °E, Ono and Moteki (2013, 2017) found *S. thompsoni* to be distributed between the surface and 2,000 m depth, noting an increase in surface abundances at nighttime. High *S. thompsoni* abundances in these studies were typically associated with warm Modified Circumpolar Deep Water. In a complimentary study reporting the depth distributions of Antarctic krill species (Ono et al. 2011), offshore adult *E. superba* were also widely distributed between the surface waters and ~2,000 m depth. In this study, the 140 °E line of longitude was identified as a region of potential broad-scale habitat overlap between *E. superba* and *S. thompsoni*. Based on the 24-hour vertical distributions reported by Ono and Moteki (2013, 2017), it is reasonable to assume that some degree of water column overlap between salps and offshore adult *E. superba* was occurring. Future studies investigating the vertical distributions of both *S. thompsoni* and *E. superba*, and how these species utilise discontinuities in the water column, will prove key in identifying the true extent of habitat competition in regions where horizontal overlap is evident. In addition, it is important to understand the biological mechanisms that might underpin avoidance behaviour between *E. superba* and *S. thompsoni*.

Kawaguchi and Takahashi (1996) identified *E. superba* as an *S. thompsoni* predator, while it was earlier suggested that *S. thompsoni* produce a distasteful metabolic product capable of deterring *E. superba* (Fraser 1962).

Prey source overlap between Salpa thompsoni and Euphausia superba

Persistent vertical overlap of *S. thompsoni* and *E. superba* habitat is likely to introduce or intensify *S. thompsoni/E. superba* prey overlap. *S. thompsoni* (0.1 µm feeding mesh diameter (Bone & Trueman 1983)), is a generalist omnivore: with prey items including diatoms, silicoflagellates, tintinnids and cyclopoid copepods (Hopkins & Torres 1989, Lancraft et al. 1991). Adult *E. superba* (2–3 µm mesh size; Schmidt and Atkinson (2016)), are more selective in their feeding, preying primarily on diatoms, as well as ingesting prymnesiophytes and cryptophytes (Haberman et al. 2003). Results from this study show that, in the Kerguelen Plateau (a region of potential horizontal and vertical habitat overlap) there was significant dietary overlap between *S. thompsoni* and *E. superba*. At target trawl 15, *S. thompsoni* ingested thirty taxonomic groups, including the full spread of *E. superba* prey sources (nineteen taxa). Furthermore, both *S. thompsoni* and *E. superba* shared the same primary food source: *Fragilariopsis* diatoms.

Currently, there is no evidence to show that interspecific competition for *Fragilariopsis* diatoms is limiting the availability of this prey source for *E. superba*. Climate-driven changes in zooplankton assemblages, however, will shape future food availability for both *S. thompsoni* and *E. superba*, with the potential to heighten competition for prey items shared by the two species. Projected responses of Southern Ocean diatoms to climate change vary; increases in iron and temperature may drive more rapid diatom growth (Boyd et al. 2016), while warmer temperatures and lower pH

may continue to shift the Southern Ocean phytoplankton community from a diatom-based assemblage to a flagellate-based assemblage (Deppeler & Davidson 2017). Judging by the typical prey size distributions within *S. thompsoni* and *E. superba* diets, a smaller Southern Ocean phytoplankton community will provide *S. thompsoni* a "competitive edge." Phytoplankton less than 1 μm in size can metabolically satisfy gelatinous tunicates (Sutherland et al. 2010), while, conversely, krill feed most efficiently on prey >10 μm and are unable to capture prey smaller than 6 μm (Kawaguchi et al. 1999). In a changing Southern Ocean, *E. superba* populations are predicted to experience significant climate-driven changes in broad-scale sea-ice habitat (Melbourne-Thomas et al. 2016, Piñones & Fedorov 2016), and competition with *S. thompsoni* for both diatoms and high-latitude habitat will only amplify existing survival pressure.

It must also be noted that, based on recent dietary analysis of West Antarctic *S. thompsoni*, flagellates rather than diatoms form the major component of their diet (von Harbou et al. 2011, Metfies et al. 2014). In the present study, only particles greater than 3 μm were identified in the gut content analysis, meaning small, or damaged, flagellates were unlikely to be identified. Although the gut content analysis in this study enumerated a limited number of taxa, the aim of the analysis was not to provide an absolute dietary profile, but to identify species-level dietary overlap between *S. thompsoni* and *E. superba*. For that reason, it is unlikely that unidentified prey items biased the diet overlap results of this chapter. Still, future studies investigating prey source overlap between *S. thompsoni* and *E. superba* would benefit from identifying particles in *S. thompsoni* guts smaller than 3 μm, as this would allow an estimate of what percent of *S. thompsoni* gut contents comprise items also consumed by *E. superba*.

Salpa thompsoni *and* Euphausia superba *biochemical composition*

Information on the biochemical composition of *S. thompsoni* in the Indian Sector of the Southern Ocean is scarce (Table 3.7). In this study, *S. thompsoni* carbon and nitrogen content was more variable than that of euphausiids. These *S. thompsoni* estimates were markedly higher than summer carbon and nitrogen contents previously reported in nearby Prydz Bay (Ikeda & Bruce 1986). The *S. thompsoni* biochemical composition identified in this study, was, however, similar to summer averages identified in the Lazarev Sea (Dubischar et al. 2012) and West Bellingshausen Sea and Weddell Gyre (Dubischar et al. 2006). While seasonal differences in *S. thompsoni* carbon and nitrogen content have been identified (Dubischar et al. 2006), spatial and long-term temporal variations in elemental composition must also be considered. Increased information on *S. thompsoni* life history has revealed potential spatial variation in life cycle (Pakhomov & Hunt 2017), highlighting the need to re-evaluate, and produce regionally explicit, estimates of *S. thompsoni* properties and functions.

The average carbon and nitrogen in KAXIS *E. superba* were similar to historic values of Indian Sector (Färber-Lorda et al. 2009) and Prydz Bay summer adults (Ikeda & Bruce 1986). Average carbon and nitrogen in KAXIS *E. triacantha* were also similar to earlier Indian Sector averages (Ikeda & Mitchell 1982). Concerning the elemental composition of *T macrura* and *E. frigida*, the estimates by Schmidt et al. (2003), reported only in µg ind^{-1}, are most comparable. Compared to Schmidt et al. (2003) KAXIS *T. macrura* returned very similar averages (11, 834 µg ind^{-1} carbon and 1, 864 µg N ind^{-1} (A3.2.)). Average carbon and nitrogen of KAXIS *E. frigida* (C=3,672 µg ind^{-1}, N=936.1 ug ind^{-1} (A3.2.)) were considerably lower than the estimates in Schmidt et al. (2003), however, mass ind^{-1} elemental compositions cannot be exactly compared across studies

without complete morphometrics, and information on aspects of body condition, such as lipid storage.

Table 3.7 Comparison of this study with previous studies on *S. thompsoni* carbon and nitrogen[a,b]

Taxa	Average C	Average N	Reference
Salpa thompsoni	18.4%	3.6%	This study
Salpa thompsoni	4%	1%	Ikeda and Bruce (1986)
Salpa thompsoni	20%	4%	Dubischar et al. (2006)
Salpa thompsoni	21%	5%	Dubischar et al. (2012)
Euphausia superba	49.4%	9.17%	Färber-Lorda et al. (2009)
Euphausia superba	44%	10.70%	Ikeda and Bruce (1986)
Euphausia triacantha	41.2%	11.6%	Ikeda and Mitchell (1982)
Euphausia frigida	10,340 µg	1,951 µg	Schmidt et al. (2003)
Thysanoessa spp.	12,150 µg	2,531 µg	Schmidt et al. (2003)

[a]C, carbon; N, nitrogen.

[b]C and N reported for this study is combined average across life stages.

Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ provided further evidence of trophic crossover between *S. thompsoni* and *E. superba*, and added a broader ecological perspective to this overlap. Based on $\delta^{15}N$ enrichment, the seven taxa considered were split across four trophic levels: 1; particulate organic matter, 2; *S. thompsoni* and *E. superba*, 3; *E. frigida*, *T. macrura*, and 4; *E. triacantha*. The $\delta^{13}C$ signatures of *S. thompsoni* and *E. superba* did not significantly differ, supporting the conclusion derived from the gut content analysis that the two zooplanktors were feeding on the same key prey items. Furthermore, the closeness between the *S. thompsoni* and *E. superba* C signatures and the particulate organic matter signatures suggested that the majority of the *S. thompsoni* and *E. superba* diet comprised 1.2 µm-1,000 µm phytoplankton from the water column. The *S.*

thompsoni $\delta^{13}C$ signature was considerably more variable than the *E. superba* signature (ranging between -29.70 and -23.38) and possible *S. thompsoni* prey items not encompassed by the POM size classes include radiolarians and foraminiferans (Hopkins & Torres 1989).

Existing estimates of *S. thompsoni* $\delta^{13}C$ and $\delta^{15}N$ are variable (Table 3.7). In this study, average $\delta^{13}C$ in KAXIS *S. thompsoni* fell between the estimates of Stowasser et al. (2012) and Pinkerton et al. (2013), while $\delta^{15}N$ was lower than *S. thompsoni* in these previous studies. Isotopic ratio differences in summer *S. thompsoni* and *E. superba* may be a combination of natural variation and differences in the local phytoplankton community composition. The combined average $\delta^{13}C$ and $\delta^{15}N$ ratios of the KAXIS POM size classes were -29±0.61 and 0.28±0.70, respectively. While these signatures were similar to estimates in Pinkerton et al. (2013), they were considerably lower than $\delta^{13}C$ and $\delta^{15}N$ reported in Stowasser et al. (2012), highlighting differences in phytoplankton assemblages across the Scotia Sea and the Kerguelen Plateau. Furthermore, as $\delta^{13}C$ and $\delta^{15}N$ are known to increase with chlorophyll-*a* (Kruse et al. 2015), the rate of primary production may also have driven variations in isotopic signatures across studies.

The results of Stowasser et al. (2012), Pinkerton et al. (2013) and this study also highlight spatial differences in the salp/krill trophic relationship (Table 3.7). In this study, *E. superba* individuals were more depleted in $\delta^{13}C$ and $\delta^{15}N$ than *E. superba* sampled by both Stowasser et al. (2012) and Pinkerton et al. (2013). Regarding the isotopic separation between *S. thompsoni* and *E. superba*, comparisons between this study and previous West Antarctic estimates suggest overlap in *S. thompsoni/E. superba* diet and trophic position was intensified in the 2016 Kerguelen Plateau ecosystem. In the 2008 Ross Sea community, average *S. thompsoni* and *E. superba* $\delta^{13}C$ differed by 3.1

(Pinkerton et al. (2013)), indicating greater dietary segregation (i.e. less prey sources shared by *S. thompsoni* and *E. superba*) than that of the current study. $\delta^{15}N$, however, was more similar (0.2 difference) than in the KAXIS samples, suggesting a closer trophic-level position (Pinkerton et al. 2013). In the Scotia Sea, differences in both *S. thompsoni* and *E. superba* $\delta^{13}C$ and $\delta^{15}N$ were pronounced, signifying minimal overlap in both diet and trophic position. Here, *E. superba* $\delta^{15}N$ was, on average, 1.6‰ higher than *S. thompsoni*, and average $\delta^{13}C$ was 2.2‰ higher (Stowasser et al. 2012).

In this study, $\delta^{13}C$ and $\delta^{15}N$ in *T. macrura*, *E. frigida* and *E. triacantha* were significantly higher than $\delta^{13}C$ and $\delta^{15}N$ in *S. thompsoni*, implying little resource overlap. As *T. macrura*, *E. frigida* and *E. triacantha* were all sampled from stations north of 62.47°S, it is possible sampling latitude was a confounding factor, however, the values reported in this study are in line with West Antarctic estimates (Stowasser et al. 2012). Higher $\delta^{13}C$ and $\delta^{15}N$ in these three euphausiids can also be explained by carnivorous diets: *E. frigida* feeds on microzooplankton, and *T. macrura* and *E. triacantha* feed on macrozooplankton (Cuzin-Roudy et al. 2014). Despite *T. macrura* being more widely-distributed than *E. superba* (Cuzin-Roudy et al. 2014), the ecosystem roles of this species is underappreciated (Nordhausen 1992, Kattner et al. 1996), and its interactions with *S. thompsoni* are overlooked in gelatinous/euphausiid studies. As *E. superba* distribution patterns continue to alter under a range of pressures, the ecosystem input from such "other" Southern Ocean krill, as well as their relationships with *S. thompsoni*, could prove pivotal in shaping future Southern Ocean trophic structure and ecosystem energy flow.

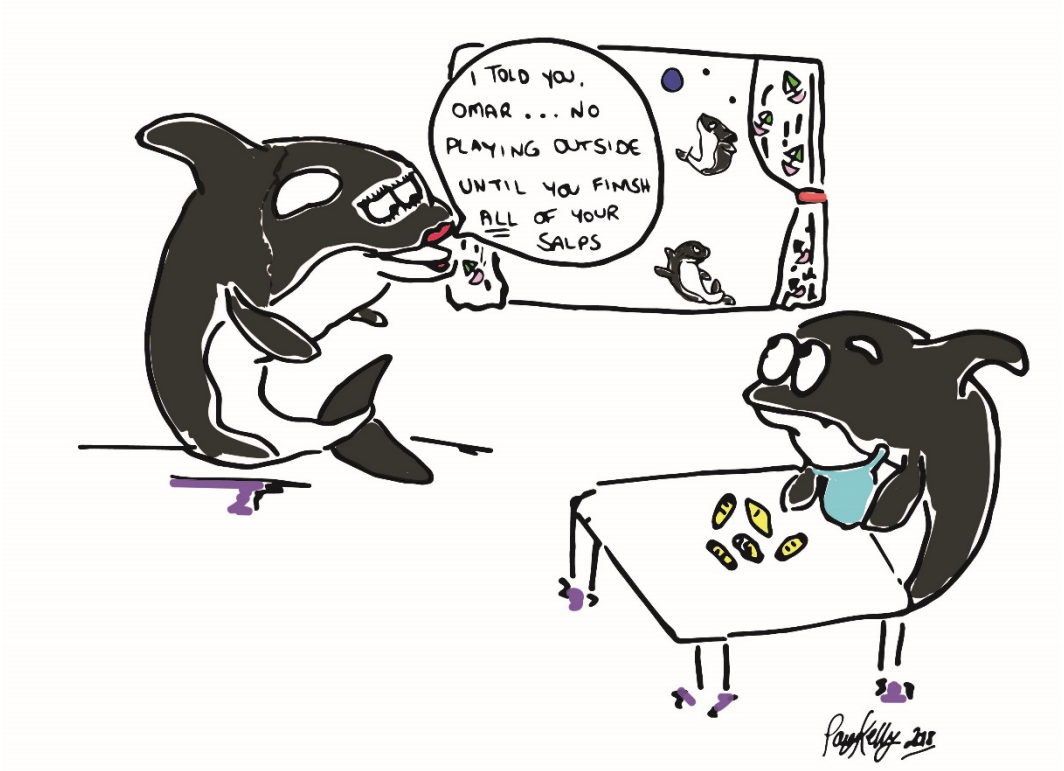
How might spatial overlap between Salpa thompsoni *and* Euphausia superba *affect higher trophic levels?*

Increased or more persistent resource overlap between *S. thompsoni* blooms and euphausiid swarms may alter the functioning of higher trophic levels, including the feeding behaviour of typical euphausiid predators. While *S. thompsoni* is a known food item of Southern Ocean albatross (Tickell 1964, Harper 1987) and fish (Raga et al. 2015), it is not clear whether they are typically incidentally or intentionally ingested. In the West Antarctic Peninsula region, Kokubun et al. (2013), used miniaturised cameras to investigate responses by Gentoo and Chinstrap penguins to *S. thompsoni* occurring in close proximity to *E. superba*, finding that the penguins rarely made an effort to catch *S. thompsoni*. Thiebot et al. (2016) undertook a similar experiment using Adelie penguins, reporting that, while individuals actively preyed upon jellyfish, salps were not targeted. In temperate regions, salps have been referred to as "survival food"; appealing to typically non-gelatinous feeders only when other traditional sources are severely limited (Mianzan et al. 2001). The conditions under which salps become an energetically favourable Indian Sector food source are unknown, and further research into fine-scale overlap between *S. thompsoni* and euphausiids is needed to improve understanding of how higher order predators are responding to increased *S. thompsoni* production. Furthermore, future research into the acoustic properties of salps may unlock key information on responses of higher order predators using echolocation for prey selection.

3.7 Conclusions

In the literature, the argument surrounding *S. thompsoni*'s role as a competitive threat to *E. superba* is split, with evidence supporting negligible competition due to

spatial segregation (Hosie & Cochran 1994, Kawaguchi et al. 1998, Pakhomov et al. 2002, Pakhomov 2004), as well as potential competition due to overlap in horizontal habitat (Bernard et al. 2012, Ross et al. 2014), vertical distributions (Ono et al. 2011, Ono & Moteki 2013, 2017) and diet (Lancraft et al. 1991). This study presents evidence of resource overlap between summer populations of *S. thompsoni* and *E. superba* in the Kerguelen Plateau region. Based on the findings of this study, *S. thompsoni* are removing *Fragillariopsis* diatoms, a major component of *E. superba*'s diet, from the water column. Furthermore, the results of this study show horizontal and vertical spatial crossover in *S. thompsoni/E. superba* populations in this region. Compared to other Southern Ocean euphausiids, Indian Sector *E. superba* is in a unique position of heightened resource overlap with *S. thompsoni*. Additional research is required to better estimate the proportion of Indian Sector *S. thompsoni* and *E. superba* populations competing for food and habitat, and the effect of this competition on *E. superba* abundances. Study efforts targeting *E. superba* population dynamics can provide crucial information on *S. thompsoni*/*E. superba* interactions, and utilising such impromptu research opportunities may prove pivotal in understanding how increased *S. thompsoni* production is altering lower trophic level composition, and the overall structure and function of the Indian Sector ecosystem.


I TOLD YOU, OMAR ... NO PLAYING OUTSIDE UNTIL YOU FINISH ALL OF YOUR SALPS

CHAPTER 4

Elemental and energetic profiles of *Salpa thompsoni* and *Euphausia superba* from the Kerguelen Plateau region of the Southern Ocean

Preface:

The Southern Ocean is undergoing considerable change in its physical and chemical environment, with habitat alterations predicted to favour gelatinous species, including the salp *S. thompsoni*. Foodweb and ecosystem models are important tools for evaluating the ecological and management implications of such changes. However a lack of in-*situ* data on the elemental and nutritional content of *S. thompsoni* often means there is not sufficient information to include *S. thompsoni* in whole-of-ecosystem models (Hill et al. 2006), leading to incomplete energy flow estimates. This study presents information on the maturity stage distribution, elemental composition and nutritional content of *S. thompsoni* from the ecologically significant, but understudied, Kerguelen Plateau region. Over one hundred *Salpa thompsoni*, collected across ten stations, were analysed. Carbon and nitrogen content (% dry weight) increased with maturity stage (from immature, to developing, to mature) by an average of 1.6 and 0.5, respectively. No distinct spatial pattern in maturity stage was identified, however, the spread of life stages may have followed a temporal trend, reflecting natural growth within the broader community. Average protein and energetic content in *S. thompsoni* was 116 µg/ml (7% dry weight), and 27 Joules ind^{-1}, respectively. A complimentary *E. superba* nutritional profile showed that *S. thompsoni* contained less than 1% of the energy of *E. superba*. Furthermore, the *S. thompsoni* protein content determined in this study was substantially less than literature estimates of some Southern Ocean copepod, cnidarian and hydrozoan species. Data from this research will allow for more comprehensive parameterisation of ecosystem models to more accurately reflect energy pathways, and to enable improved quantitative estimates of the impact of increased production of *S. thompsoni* on trophic structure and function

4.1 Highlights

- This study reports the first estimates of prey-source value, based on protein and energy content (Joules) for *S. thompsoni* in the Kerguelen Plateau region of the Southern Ocean. The nutritional profiling revealed that, in January/February 2016, *S. thompsoni* aggregates contained less than five times the protein (% DW), and less than 1% of the energy of *E. superba* (a primary food source for higher order predators in the region).
- The carbon, nitrogen and protein contents of *S. thompsoni* identified in this study, and most recent literature estimates (Dubischar et al. 2006, Dubischar et al. 2012), were markedly higher than a number of historical studies. Further research is required to determine whether this reflects a long term increase in the elemental and energetic content of *S. thompsoni* has occurred.
- While *S. thompsoni* are less nutritious than many other Southern Ocean prey sources (euphausiids, copepods and some hydrozoans and cnidarians), individuals may be energetically "cheap" to capture, due to their mass aggregations and inability to actively avoid predators. Additional studies are required to determine the energetic return of consuming *S. thompsoni*, and whether *S. thompsoni* consumption can be considered an energetically optimal foraging strategy.

4.2 Key words

Salpa thompsoni, Kerguelen Plateau, *Euphausia superba*, prey source, nutritional profiling, alternative energy pathways.

4.3 Introduction

The crustaceous zooplanktor *Euphausia superba* forms the major component of the diets of numerous species of whales, seals and penguins in the Southern Ocean. For higher-order predators that consume mostly *E. superba*, myctophids, copepods and other euphausiids can still be important food items. Because higher trophic level species rely so heavily on a limited number of prey sources, changes in the Antarctic and Southern Ocean zooplankton community composition is likely to have significant flow-on effects. Such effects include alterations to ecosystem structure and the amount of energy transferred from lower trophic levels to higher trophic levels (energy flow) (Murphy et al. 2012, Constable et al. 2017).

The biomass of *E. superba* (estimates suggest anywhere between 125-700 million tonnes (Nicol & Endo 1997)) is estimated to exceed that of any other multi-cellular organism. Despite this, on a regional basis during summer, *E. superba* densities are sometimes surpassed by that of *Salpa thompsoni*; a barrel-shaped gelatinous tunicate, also referred to as a salp (Steinberg et al. 2015). Blooms in *S. thompsoni* result from the asexual budding of solitary individuals from chains of aggregates, with discrete blooms surpassing 1,800 ind. 1,000 m^{-3} (Loeb & Santora 2012). Although *S. thompsoni* can become the most abundant (based on individuals m^{-2}) zooplanktor in a region over a very short time-scale, large aggregations are typically short-lived, with chains breaking up due to pressures such as high concentrations of phytoplankton clogging the salp feeding mesh (Perissinotto & Pakhomov 1998b). Despite the ephemeral nature of *S. thompsoni* blooms, there is evidence that the species is increasing its presence in the West Antarctic Peninsula region of the Southern Ocean, through a southerly shift in

populations and an increase in peak abundances (Atkinson et al. 2004, Ross et al. 2014, Steinberg et al. 2015). Studies identifying changing distribution patterns of *S. thompsoni* in the West Antarctic attribute increased production to warmer ocean temperatures, decreased sea-ice extent and low chlorophyll-*a*. If projected physical and chemical change in the Southern Ocean eventuate, including a 1–1.5 °C increase in the temperature of the Antarctic Circumpolar Current (Liu & Curry 2010), future conditions may strongly favour *S. thompsoni* success (Moline et al. 2004). Despite the potential for the ecosystem role of *S. thompsoni* to change significantly over the next century, the broad-scale ecological consequences of increased production remain largely unknown.

Salps have previously been considered a global energetic "dead-end" in marine ecosystems (Verity & Smetacek 1996), owing to their apparent absence in higher-trophic level predator diets (historically inferred from gut content analysis). However, recent advances in diet analysis methods, including stable isotope analysis and DNA analysis have revealed *S. thompsoni* to be a prey source for Antarctic fish and seabirds (Yves et al. 2002, Raga et al. 2015) and, therefore, an effective pathway for energy transfer from primary producers to higher-order predators. While alternative energy pathways (those not centered on *E. superba*) are considered important for ecosystem structure and resilience, they are unable to match the energy transfer of *E. superba* (Murphy et al. 2016). Consequently, any shift from an *E. superba*-based foodweb to a *S. thompsoni*-based foodweb may compromise the capacity of the Southern Ocean ecosystem to maintain current higher order predator biomass (Murphy et al. 2007, Murphy et al. 2016).

The energetic efficiency of an *S. thompsoni* pathway is yet to be quantified, partly owing to several uncertainties surrounding when, and why, *S. thompsoni* might be advantageous prey. In some temperate regions, salp species are referred to as "survival food", appealing only when preferred food sources are absent (Mianzan et al. 2001). In the Southern Ocean, it is important to distinguish species-specific responses of potential predators of *S. thompsoni*. For example, Gentoo and Chinstrap penguins, typical euphausiid predators, have been observed dodging *S. thompsoni* chains that are in close proximity to *E. superba* swarms (Kokubun et al. 2013). Conversely, grey-headed albatrosses, a more generalist feeder, actively prey upon *S. thompsoni* blooms (Paulo et al. 2004).

To obtain an improved estimate of the potential impact of increasing *S. thompsoni* abundances on energy flow through the Southern Ocean ecosystem, up-to-date and spatially explicit information on fundamental *S. thompsoni* properties, including distribution and nutritional content, is required. Chapter 2 of this thesis detailed historic and recent *S. thompsoni* distribution patterns across the Kerguelen Plateau region, while this chapter provides a comprehensive account of the energetic potential of *S. thompsoni* in the Kerguelen Plateau region. Regarding biochemical composition, *S. thompsoni* is composed of lipids (~6% in aggregates and ~7% in solitaries) and proteins (~5-9% in aggregates and ~8% in solitaries). Carbohydrates (~1% in solitaries and aggregates), fatty acids and cholesterol are also present (Mimura et al. 1986, Dubischar et al. 2006, Dubischar et al. 2012). Literature estimates of *S. thompsoni* nutritional value are, however, highly variable (see results of Huntley et al. 1989, Clarke et al. 1992, Dubischar et al. 2006), with the theory of "missing components" providing possible explanations. In their analysis of *S. thompsoni* energetic content, Dubischar et al. (2006)

found that, after analysis of proteins, lipids, carbohydrates and ash, one third of the dry weight of *S. thompsoni* was unaccounted for. This "missing third" was attributed to unidentified organic proteins and glycoproteins, as well as residual water not removed during the drying process. Furthermore, *S. thompsoni* water content accounts for more than 90% of total weight (Dubischar et al. 2006), complicating the determination of dry weight, and subsequent nutritional value.

Variation in the biochemical content of *S. thompsoni* across studies may be representative of temporal and spatial variation in fundamental properties in the species. Furthermore, recent reports of differing *S. thompsoni* growth rates across the West Antarctic (Pakhomov & Hunt 2017) highlight spatial variation in life history, as well as the need for regionally explicit estimates of *S. thompsoni* features (e.g. biochemical composition) and processes (e.g. growth and reproduction). Current knowledge of *S. thompsoni* distribution patterns, life history and energy content is concentrated off the West Antarctic Peninsula (e.g. Atkinson et al. 2004, Loeb & Santora 2012, Steinberg et al. 2015), leaving the East Antarctic, including the commercially and ecologically significant Indian Sector, understudied. The Indian Sector encompasses a highly valuable toothfish and icefish industry, and krill harvesting is permitted in the westernmost waters, within Area 58 (CCAMLR 2018a). Furthermore, there are various Indian Sector hotspots for productivity, including the Kerguelen Plateau, where concentrated *E. superba* abundances provide an optimal feeding and breeding ground for Southern Ocean whale species (Tynan 1998).

To maintain ecosystem structure in the face of altering *E. superba*/*S. thompsoni* abundance ratios, the changing role of *S. thompsoni* in the Indian Sector must be

examined, and the energetic potential of the species quantified. This study presents the first *S. thompsoni* population morphometrics and protein and energy-based nutritional profile for the Kerguelen Plateau region, while also providing corresponding *E. superba* population morphometrics and protein and energy content. This new and essential information will allow for more accurate *S. thompsoni* vs. *E. superba* energy pathway comparisons, and, consequently, more representative ecosystem models (which typically overlook or underestimate gelatinous organisms). Furthermore, research that reduces important uncertainties and gaps in assessments (i.e. assessments of changing ecosystem structure and function) is considered a priority for science to be integrated into policy. This research may, therefore, aid in the development of effective strategies by management organisations such as CCAMLR, that are currently hindered by knowledge gaps in our understanding of alternative energy pathways (Constable et al. 2017).

4.4 Methods

2016 Kerguelen axis (KAXIS) Salpa thompsoni *and* Euphausia superba *sampling locations and field methods*

Salpa thompsoni and *E. superba* data were collected during the 2016 Kerguelen Axis (KAXIS) voyage. From January 22 to February 16, the KAXIS voyage track crossed major oceanographic features, including the Southern Boundary of the Antarctic Circumpolar Current and the Southern Antarctic Circumpolar Current Front. The majority of the KAXIS sampling was concentrated in the region of the sea-ice edge near the Princess Elizabeth Trough and Southern BANZARE Bank, between 70 and 91°E (Fig. 4.1). The zooplankton community was sampled through 40 “Routine Trawls” and 30

"Target Trawls," using an 8 m^2 RMT 8 net of 4.5 mm mesh (Baker et al. 1973). Routine trawls were oblique tows, returning an integrated sample across a depth range of ~10-200 m. Each routine trawl covered an average horizontal distance of 1,200 m, over the course of 20-45 minutes. Target trawls were directed at an acoustic target suggesting the presence of a krill swarm, sampling a ~10-25 m depth range, over 5-15 minutes. *Salpa thompsoni* data for this chapter were collected during Routine Trawls 00, 03, 05, 08, 10, 12, 13, 15, 18, 23, 26, 28, 30, 31, 32, 34, 38, 40, 42, and Target Trawl 25. *Euphausia superba* data for this chapter were collected at Target Trawls 14 and 16 (Fig. 4.1, Table A4.1). *Salpa thompsoni* and *E. superba* data collected during the remaining trawls were used to investigate distribution patterns, population structure and environmental drivers (Chapter 2), and stable isotope and gut content analysis (Chapter 3). Across all Routine Trawls, the *S. thompsoni* populations, if present, comprised 90% aggregates and 10% solitaries (Chapter 2). Due to the scarcity of solitaries, only aggregates were used for analysis in this study.

Once *S. thompsoni* aggregates were retrieved, total length and oral-atrial length (body cavity end-to-end) were recorded and a maturity stage was assigned (Table A4.2). Maturity stage was allocated after observing the ovaries, and consulting the length-maturity stages of Loeb and Santora (2012). Where possible, a subsample of 20-50 aggregates was selected for morphometrics. Upon collection, *E. superba* wet weight and maturity stage (based on length and gonad development) were recorded. Together with *E. superba*, *S. thompsoni* individuals were snap frozen in liquid nitrogen, and stored at 80°C.

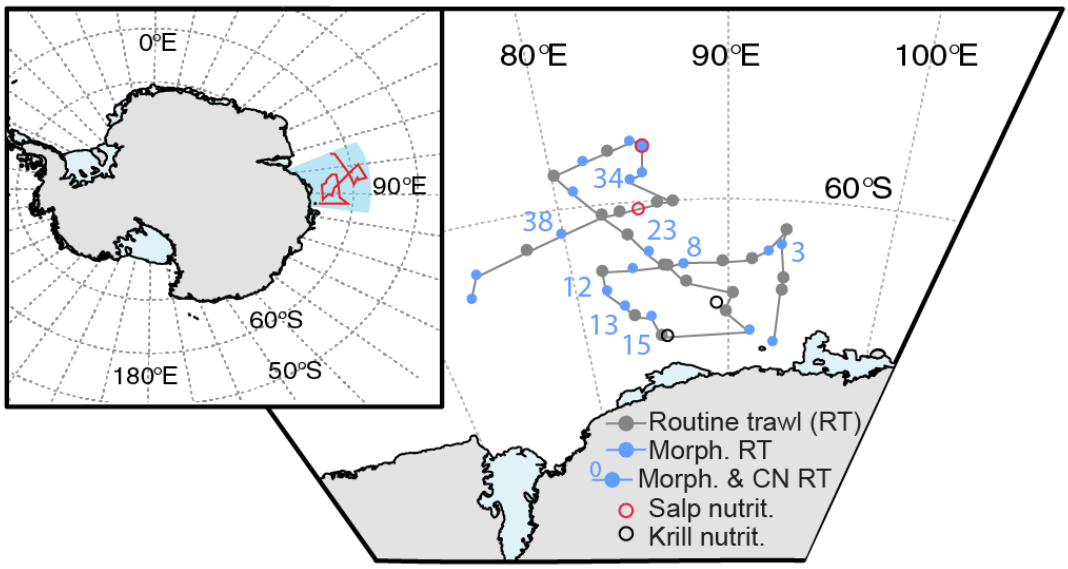


Figure 4.1 (left) Location of the Kerguelen Axis study region (blue area) with respect to the Antarctic continent and (right) Kerguelen Axis voyage track. Solid circles connected by lines denote routine trawls. Filled blue circles represent routine trawls (RT) where *Salpa thompsoni* morphometrics (Morph.) were recorded. Filled blue circles with an adjacent number denote routine trawls where both morphometrics were recorded, and samples for elemental analysis (CN) collected. Red rings are locations where *S. thompsoni* were sampled for protein and energy content (Salp nutrit.), and black rings are locations where *E. superba* were sampled for protein and energy content (Krill nutrit).

Salpa thompsoni *carbon and nitrogen content*

For elemental analyses, *S. thompsoni* individuals were selected from Routine Trawls 3 (n=9), 8 (n=11), 12 (n=11), 13 (n=10), 15 (n=7), 23 (n=9), 34 (n=9), 38 (n=10) (Table A4.2). Frozen *S. thompsoni* were thawed at room temperature, rinsed with Milli-Q water, weighed (wet weight) and then oven dried at 60°C until a stable mass was reached (12–24 hours). Dry mass was then recorded. Dried individuals were ground to a fine powder, and 0.3–0.9 mg extracted for analysis. Elemental composition was

determined via an Isoprime100 Elemental Analyser, in NCS combustion mode. In total, the carbon and nitrogen content of 6 immature aggregates, 34 developing aggregates and 36 mature aggregates were determined.

Salpa thompsoni *energy content*

Energy content (in Joules (J)) was determined for mature *S. thompsoni* aggregates, collected at T25 (n=5) and R31 (n=3), and for adult *E. superba* males, collected at T14 (n=6) and T16 (n=5) (Table A4.2). Combined maturity stage results are reported for trawls T25 and R31. Frozen *S. thompsoni* and *E. superba* were thawed at room temperature, rinsed with Milli-Q water, weighed (wet weight) and then oven dried at 60°C until a stable mass was reached (12- 24 hours). Dry mass was then recorded. Dried individuals were ground to a fine powder and combined with benzoic acid to make a pellet ranging from 100–200 mg. Energetic content of the organic material in the pellet was determined using a 22 ml oxygen bomb, as part of a Parr 6725 Semimicro Oxygen Bomb Calorimeter. Error of calorimeter output was estimated at <1.0% of measured value for samples releasing less than 100 calories (420 J).

Protein content

For protein content, mature *S. thompsoni* aggregates were sampled at T25 (n=5) and R31 (n=7), while *E. superba* (14 adult males and one juvenile) were sampled at T14 (n=8) and T16 (n=6). Frozen *S. thompsoni* and *E. superba* were thawed at room temperature, rinsed with Milli-Q water, weighed (wet weight) and then freeze-dried for ~24 hours until a stable weight was reached. Dry weight was then recorded. For the nutritional profiling results of this study to be most compatible with the results of

previous studies (Dubischar et al. 2006, 2012), guts of *S. thompsoni* and the krill species were also not removed prior to analysis.

Protein content of both *S. thompsoni* and *E. superba* were measured using the Bradford protein assay (Bradford 1976), with a bovine serum albumin standard. Protein content was inferred from absorbance at 595 nm, measured using a FLUOstar Optima Spectrophotometer. Where possible, both energy and protein content were analysed for a single individual, however, often this was not possible due to the small amount of biological material.

Statistical analysis and figures

Using R version 3.5.1 (R-Core-Team 2018), a one-way ANOVA (Analysis Of VAriance, testing the significance of differences between elemental composition across *S. thompsoni* life stages) and figures were executed using the packages "ggplot2" (Wickham 2016), "marmap" (Pante & Simon-Bouhet 2013), "scatterpie" (Guangchuang 2018), "orsifronts" (Orsi et al. 1995), and "raster" (Hijmans 2018).

4.5 Results

Distribution patterns of Salpa thompsoni *maturity stages*

Across the 19 morphometrics stations, the majority of *S. thompsoni*, 52% (n=396), were classified as developing. Immature aggregates accounted for 26% (n=202) of the total population, and mature aggregates 22% (n=166) (Fig. 2, Table A4.1.). Although total abundance was highest for developing aggregates, immature aggregates were most widely distributed, present in all but two morphometrics trawls. Furthermore, trawls R0, R05, R10, R26 consisted solely of immature aggregates. Developing

aggregates were present in 14 of the 19 morphometrics trawls and accounted for no more than 83% (R38) of a single trawl. Mature aggregates occurred at 13 morphometric locations and accounted for up to 73% (R13) of a trawl's assemblage. Based on the morphometrics trawls, no maturity stage was delineated by an exclusive east-west or north-south boundary. There were, however, broader patterns, including trawls of >50% mature aggregates occurring solely south of 62 °S, and 100% immature aggregates retrieved along the 93 °E line of longitude (Fig. 4.2). In addition, the maturity stage composition of some neighbouring trawls differed substantially, highlighting the spatial patchiness of *S. thompsoni* population dynamics. Such small-scale (spatial) variability was present between trawls R0 (65.46 °S, 93.18 °E), which comprised all immature aggregates, and R18 (65.04°S, 91.50°E), which captured both developing (67%) and mature (33%) aggregates. Similarly, R10 (62.53°S, 89.91°E) comprised all immature aggregates, while R23 (61.94 °S, 85.03 °E) sampled mostly developing (53%) and mature (28%) aggregates. It is important to note that while these trawls were close in a spatial sense, ten days separated sampling at R0 and R18, and eleven days separated sampling at R10 and R23. Consequently, it is likely that the *S. thompsoni* community developed considerably over these periods, introducing variation across spatially close trawls.

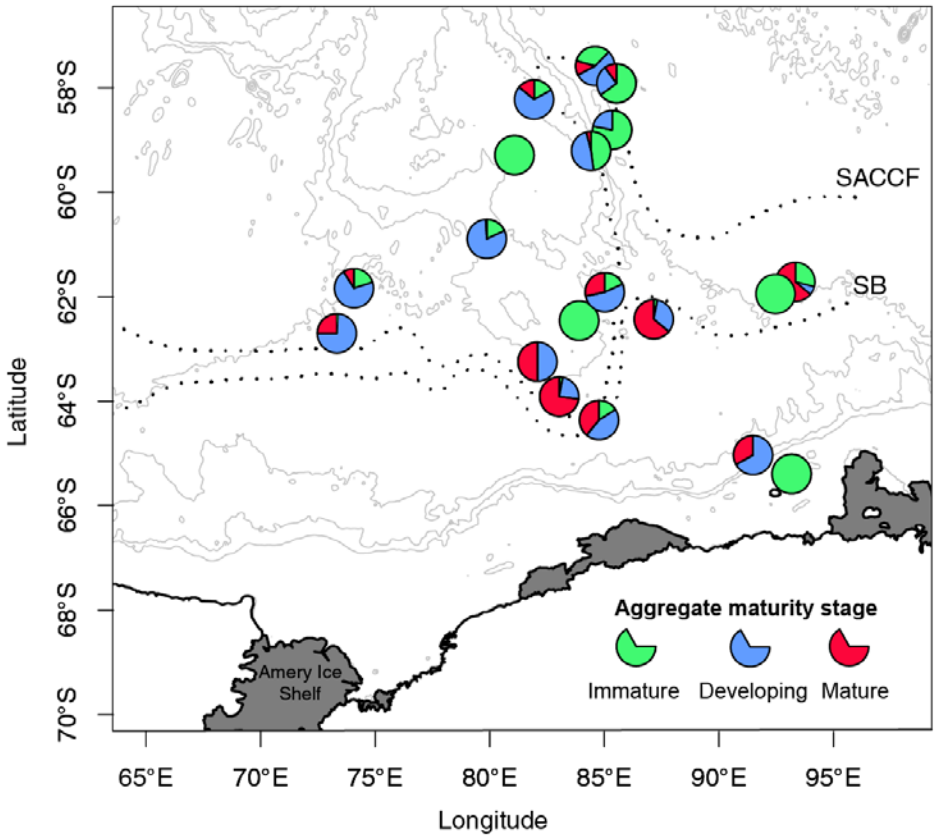


Figure 4.2 Maturity stage composition of *Salpa thompsoni* aggregates, across morphometrics trawls. Maturity stages (immature, developing and mature) are proportions of the morphometrics subsample. SACCF, Southern Antarctic Circumpolar Current Front; SB, Southern Boundary of the Antarctic Circumpolar Current.

Length-weight dynamics, and elemental composition, of aggregate Salpa thompsoni

Across maturity stage, dry weight accounted for 5.5-6.2% of wet weight on average (Figs. 4.3a, b; Table A.4.2), with the average %DW/WW significantly increasing from immature to mature *S. thompsoni* (Table 1). The wet weight of immature, developing and mature *S. thompsoni* varied between 1-179, 44-871, and 82-1135 mg, respectively. Overall, $\log_{10}$(oral-atrial length) explained around 60% of $\log_{10}$(wet weight) variation in aggregates (Fig. 4.3a). Based on the fitted linear model for the combined

population, a 1.67 unit increase in $\log_{10}$(wet weight) is expected for each one unit increase in $\log_{10}$(oral-atrial length). Dry weights of immature, developing and mature salps varied between 1-13, 2-180, and 4-99 mg, respectively. Similar to wet weight, oral-atrial length explained approximately 60% of the variation in combined aggregate dry weight (Figure 4.3b). The linear model fitted to the overall population suggested that a one unit increase in $\log_{10}$(oral-atrial length) would result in a 1.8 unit increase in $\log_{10}$(dry weight).

Both carbon and nitrogen (mg) showed an overall increasing trend with aggregate maturity stage (Figs. 4.4a, b), however, these were not statistically significant (Table 4.1). In immature *S. thompsoni*, carbon and nitrogen averaged 1.02 mg (range=0.08-1.23) and 0.20 mg (range=0.02-0.42), respectively. The average carbon and nitrogen contents in developing *S. thompsoni* were 3.48 mg (range=0.57-32.54) and 0.69 mg (range=0.1-6.55), respectively, while, in mature *S. thompsoni*, carbon averaged 6.12 mg (range=0.73-21.02) and nitrogen averaged 1.27 mg (range=0.13-4.24) (Figs. 4.4a, b, Table A4.2). From immature to mature aggregates, the % of dry weight accounted for by carbon and nitrogen increased from 16.15 to 19.28%, and from 3.0 to 3.94%, respectively (Table 4.1). The overall carbon/nitrogen ratio across the overall population ranged between 3.45 and 6.50, however, the average ratios across maturity stages were consistent, varying between 5.02 (mature individuals) and 5.29 (developing individuals).

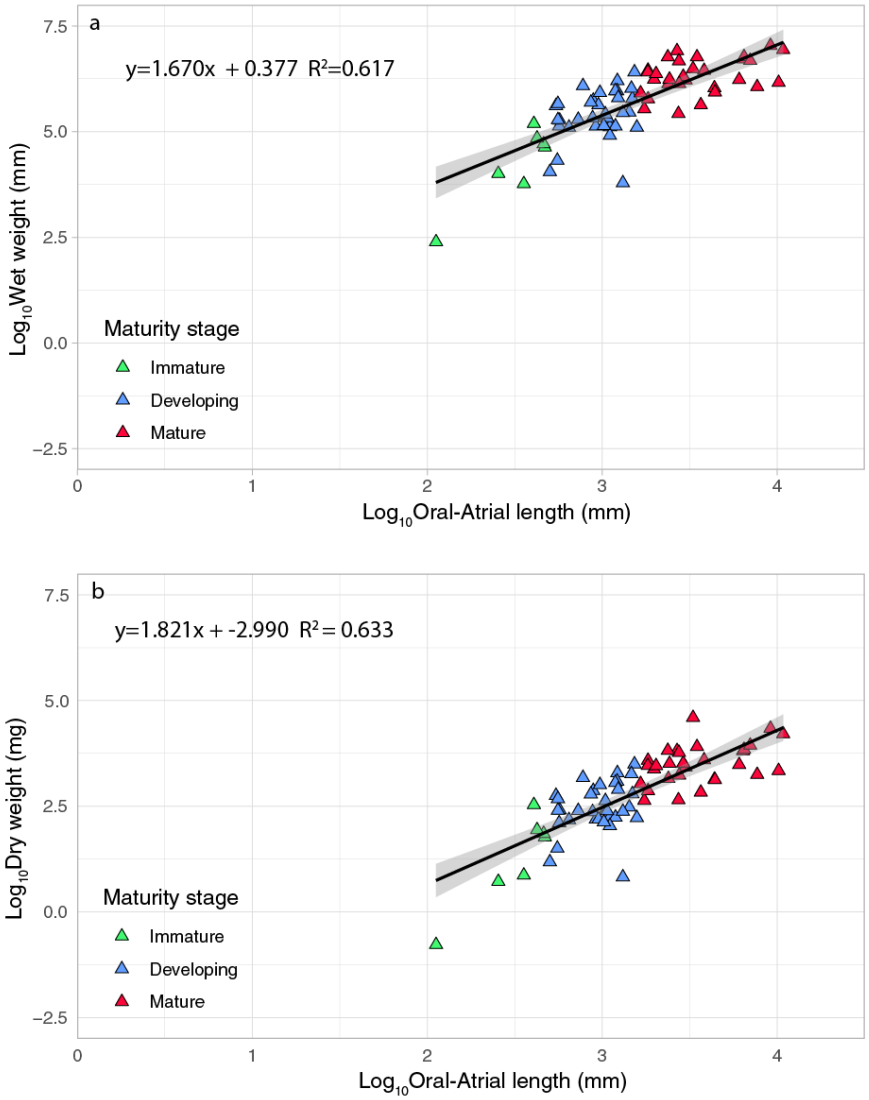


Figure 4.3a-b Log_{10} transformed *Salpa thompsoni* wet weight (a) and dry weight (b) vs. log_{10} transformed oral-atrial length. A fitted linear relationship is represented by a solid black line, and corresponding equation. The grey shaded area surrounding the linear line represents 95% confidence intervals. Immature, developing and mature *Salpa thompsoni* are coloured to visualise spread of length and weight with maturity stage. Both weight and length were log_{10} transformed, as per Bronstein and Loya (2014).

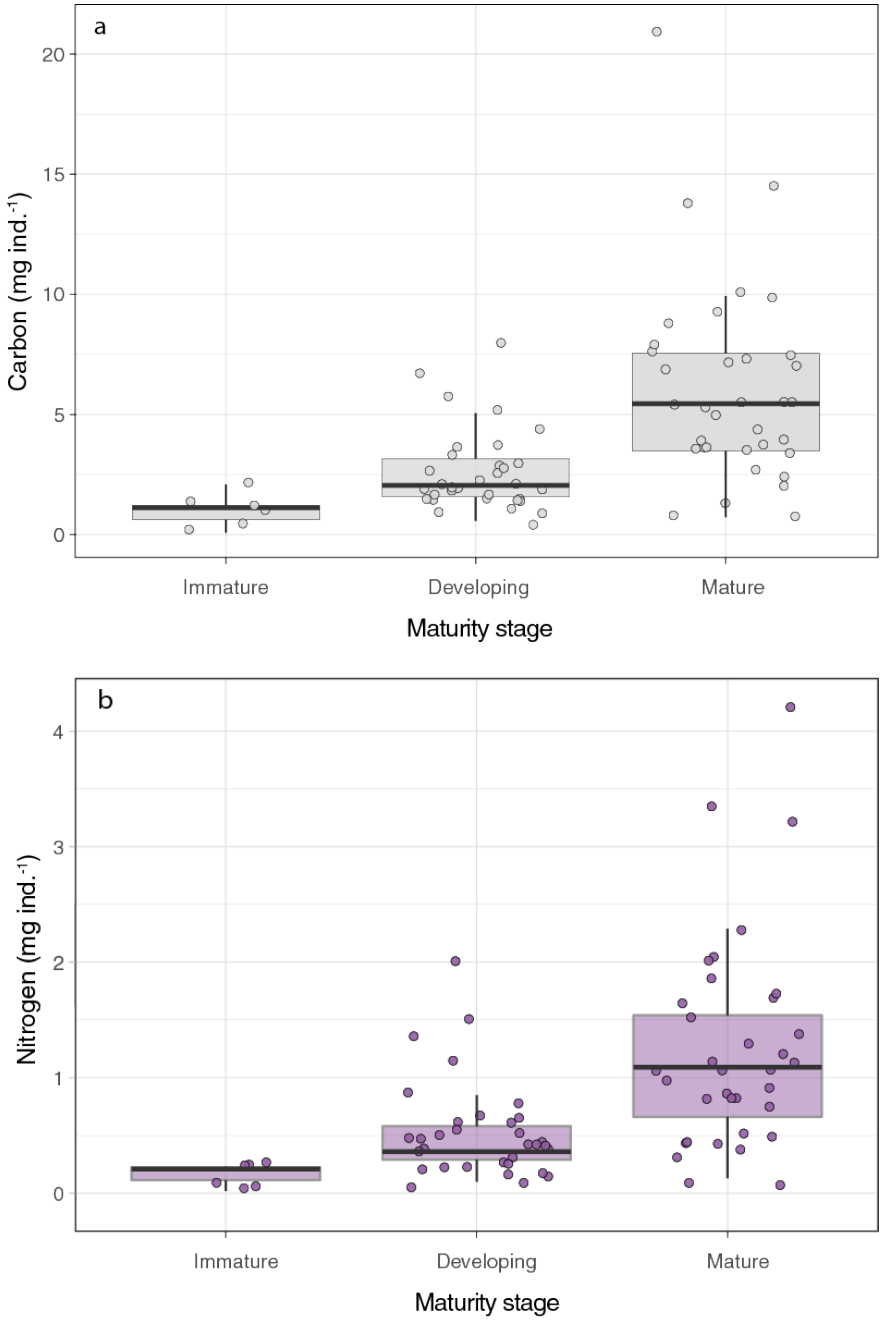


Figure 4.4a,b Box and whisker plots of carbon (a, mg ind.$^{-3}$) and nitrogen (b, mg ind.$^{-3}$) across *Salpa thompsoni* maturity stages. Within the "boxed" areas, the lower bounds mark the 25th percentile, the centre horizontal line mark the 50th percentile, and the upper bounds mark the 75th percentile. Filled circles are data points.

Table 4.1 Dry weight (DW), wet weight (WW), carbon (C) and nitrogen (N) content of *Salpa thompsoni* aggregates, across maturity stages.

	Immature (n=6)	Developing (n=34)	Mature (n=36)	*P*
% DW/WW	5.5 ± 1.0	6 ± 3.10	6.2 ± 1.80	0.02
Carbon (% DW)	16.15 ± 4.76	18.2 ± 3.30	19.28 ± 4.75	0.33
Nitrogen (% DW)	3.0 ± 0.90	3.5 ± 0.91	3.94 ± 1.23	0.14
C/N (molar)	6.04 ± 0.66	5.29 ± 0.53	5.02 ± 0.62	0.10

[p]One-way ANOVA (physical property~maturity stage) p-value, with significance at the 0.05 level.

Nutritional profiling of Salpa thompsoni *and* Euphausia superba

The energy and protein nutritional profiles confirmed *S. thompsoni* in the Kerguelen region to have, on an individual basis, an energetic content substantially lower than that of *E. superba.* (Table 4.2, Table A4.3). In mature *S. thompsoni* aggregates, the average energy content was 26.64 ±11.40 J. The average energy content of adult male *E. superba* was more than 100 times that of an *S. thompsoni* individual, at 2,922.91 (±788.94) J ind^{-1}. The energy content of adult male *E. superba* was variable, ranging between 1,817 and 4,087 J ind^{-1} (12.3-20.3 J mg^{-1} (DW)). The protein content of *S. thompsoni* was lower than that of *E. superba*, however, protein content was more similar across the two species than energy content (Table 2, Table A4.3). Raw protein of developing and mature *S. thompsoni* aggregates ranged from 0.13-2.46 mg ind^{-1} (DW), with an average of 1.09 (± 0.75) mg ind^{-1} (DW). Protein content in *S. thompsoni* was lower than that of juvenile and adult *E. superba*, which ranged from 6.57-109.95 mg ind^{-1} (DW), with an average of 62.42 (± 34.01) ind^{-1} (DW). Protein in *S. thompsoni*, on average, accounted for 9.3% (± 2.74) of an individual's DW, while *E. superba* protein accounted for 42% (±9.8).

Table 4.2 Nutritional profile (energy and protein content) of *S. thompsoni* aggregates[a], and *E. superba*[b].

	n	*S. thompsoni*	*n*	*E. superba*
Energy content (Joules ind^{-1})	mat.=8	26.64 ± 11.40 (range=13.08–46.0)	a.m.=11	2,922.71 ± 788.94 (range=1817.0–4,087.0)
Protein (µg/ml)	mat.=10 dev.=2	115.71 ± 66.87 (range = 25.19–288.30)	a.m.=13 juv.=1	287.74 ± 163.85 (range=104.78–454.05)
Protein (mg ind^{-1})	mat.=10 dev.=2	1.09 ± 0.75 (range=0.13–2.46)	a.m.=13 juv.=1	62.42±34.01 (range=6.57–109.95)
Protein (% DW)	mat.=10 dev.=2	7.35 ± 2.50 (range=1.74–10.31)	a.m.=13 juv.=1	41.95 ± 9.80 (range=28.76–55.28)

[a]mat., mature; dev., developing.
[b]a.m., adult male; juv., juvenile.

4.6 Discussion

To our knowledge, prior *in-situ* data on the heat capacity of *Salpa thompsoni* are non-existent, with current literature estimates inferred from alternate energetic properties. Based on protein, lipid and carbohydrate content, Dubischar et al. (2006) predicted an *S. thompsoni* individual of 10 g WW to possess approximately 2,037 J. Considering it would take a predator approximately 1,554 J to heat a 10 g high water-content prey item to a digestible 37°C (Wilson & Culik 1991), *S. thompsoni*, if able to provide 2,037 J, may be an energetically viable food source. In this study, *S. thompsoni* energetic content ranged between approximately 13.1-46 J ind^{-1}, and WW of the majority of individuals did not exceed 1 g. Based on the morphometrics results of this study and Dubischar et al. (2006), a 10 g WW is extremely generous, and atypical for *S. thompsoni* aggregates. A 1-2 g range would appear to be a much more appropriate WW baseline for determining, and discussing, energetic potential. If we use this more modest weight range, the original 2,037 J ind^{-1} estimated by Dubischar et al. (2006) could be

reduced to less than 210 J ind.$^{-1}$, only marginally exceeding the 156 J (assuming 37 calories used per gram of food heated) required to metabolise a 1 g *S. thompsoni*. For that reason, while *S. thompsoni* are of reasonable nutritional value, their small size and high water content means that, for an absolute energetic benefit, a predator is likely to need to consume an incredibly large number of individuals. Furthermore, any energetic payoff will not only depend on energy required to heat *S. thompsoni* to a metabolic temperature, but also on energy invested in prey capture. Models based on optimal foraging theory (Pyke 1984),which assumes a predator will select its prey based on a favourable trade-off between energy spent foraging and handling prey, and energetic content of prey, have been employed to understand the dietary choices and foraging mechanisms of Southern Ocean higher order predators (Masello et al. 2010, Doniol-Valcroze et al. 2011). What is unclear, however, is when, and in which species, selecting *S. thompsoni* as prey can be explained by optimal foraging. For higher order predators, while *S. thompsoni* might be less nutritious than other food sources, it might also be energetically "cheap" to capture as it is available in mass numbers and (unlike *E. superba*) cannot actively avoid predation. Further research is required to determine the absolute energetic favourability of consuming *S. thompsoni*, and how this varies with both bloom and individual *S. thompsoni* size.

In this study, dry weight, and carbon and nitrogen content increased with size of an individual, however, the increase was only significant in DW. The DW of aggregate *S. thompsoni* in this study accounted for 5-6% of the WW, most similar to recent estimates of Dubischar et al. (2006) and Dubischar et al. (2012) (Table 4.3). The % DW/WW of this study, and those of Dubischar et al. (2006) and Dubischar et al. (2012) were higher than earlier estimates (Table 4.3). Similarly, the carbon/DW (16-19%) and nitrogen/DW (3-

4%) estimates recorded here were in line with most recent literature, but were substantially higher than a number of historic studies. As the earlier (1982-2004) studies sampled summer *S. thompsoni* populations, and Dubischar et al. (2006) sampled during the winter, the latter authors suggested seasonal differences as a primary driver of variation in elemental content across studies. The body composition reports of Dubischar et al. (2012) and those in this study are from summer populations, discounting variation due to seasonal differences. Instead, these elevated (in comparison to 1982-2004 studies) dry weight, carbon and nitrogen estimates may provide evidence of a potential rise in organic content of summer *S. thompsoni*. It is speculated that most of the energy content of *S. thompsoni* is derived from an individual's gut (Gili et al. 2006), and nutritional profiling of isolated *S. thompsoni* guts may reveal key information on how the diet of the species can change the organic content, and prey potential, of an individual. In addition, if comprehensive morphometrics measurements (e.g. Chapter 2) are recorded in future studies of *S. thompsoni* biochemical properties, then linkages between variation in body composition and variation in physical parameters (extending beyond length) will be able to be established.

The protein content (~7%/DW) derived in this study was markedly higher than earlier (1982-2006) aggregate estimates (Table 4.3). Protein content, however, was similar to the most recent reports of aggregate nutritional content in Dubischar et al. (2012). This discrepancy across aggregate estimates may be due to sampling different life stages. In the present study, mostly mature aggregates were analysed for protein content, while many of the *S. thompsoni* sampled by Dubischar et al. (2006) were less than 20 mm in length, and were likely to be immature aggregates. Furthermore,

Dubischar et al. (2012) (who recorded the protein content most similar to this study) analysed *S. thompsoni* of 25 mm length, and these individuals were likely to have been developing or maturing individuals. It is also possible this variation reflects regional differences, as the body composition estimates in this study are the first for the Kerguelen Plateau region, requiring West Antarctic studies to be used as reference points. Repeated East and West Antarctic sampling is required to clarify any spatial influence. This study did not identify any distinct spatial trend in size (categorised by maturity stage), however, the distribution of immature, developing and mature *S. thompsoni* was likely following a temporal trend. Mature *S. thompsoni* were mostly sampled during the last half of the sampling regime, signalling an impending peak in aggregate size (and maturity stage), and subsequent aggregate nutritional content.

Table 4.3 Comparison of this study with previous studies on *Salpa thompsoni* body composition[a,b].

DW/WW (%)	C/DW (%)	N/DW (%)	Protein (% DW)	Reference
5.9	17.9	3.5	7.3	This study
6.4	17.4	3.53	4.4	Dubischar et al. (2006)
7.5	20.3		9.2	Dubischar et al. (2012)
3.8	4.7	1.2		Ikeda and Mitchell (1982)
4	4.5	1		Ikeda and Bruce (1986)
4	10			Reinke (1987)
4.3	3.4	1		Huntley et al. (1989)
3.3	6	1.5		Iguchi and Ikeda (2004)

[a]DW, dry weight; WW, wet weight: C, carbon; N, nitrogen.

[b]Body composition reported for this study is combined average across life stages.

To appreciate the potential of *S. thompsoni* as an alternative Southern Ocean food source, its energetic content must be placed in the context of that of a preferred food source, such as *E. superba*. The nutritional analyses in this study present Kerguelen Plateau *S. thompsoni* as a prey source with, generally, less than 50% of the protein, and less than 1% of the energy content of *E. superba*. It is important to note that *E. superba* (and any food source) requires heating after consumption, and that *E. superba* has a relatively high water content (around 80%). The high protein (40-80%/DW) and lipid (15%/DW) (Grantham 1977, Clarke 1984, Meyer et al. 2010) content of *E. superba*, however, compensates for this relatively high water content. In this study, protein content in adult (n=13) and juvenile (n=1) *E. superba* ranged between 28.76 - 55.28% DW, and was lower than a number of historical studies (Grantham 1977, Färber-Lorda et al. 2009, Gigliotti et al. 2011) (Table 4.4). These protein results are, however, in line with Meyer et al. (2010), who analysed protein in late spring and autumn adult *E. superba*. Regarding energy content, in this study, individual *E. superba* contained 1,817-4,087 J. This range overlaps with the energy content of Färber-Lorda et al. (2009) measured for juvenile *E. superba*, and is only slightly lower than the protein content the same study found in adult male *E. superba*. Across the literature, there is obvious variation in *E. superba* protein and energy content, with age, physiological condition, location, season, sex and diet acknowledged as variables driving inconsistencies in body composition (Gigliotti et al. 2011). As the results of this study are within the "ballpark" of multiple existing estimates, we can be confident that discrepancies between this study's *E. superba* nutritional profile and previous profiles are not due to methodological differences, but are likely a reflection of spatial and seasonal variation.

Table 4.4 Comparison of this study with previous studies analysing *Euphausia superba* nutritional content[a].

Taxa	Protein (% DW)	Energy (Joules ind^{-1})	Reference
E. superba adult male (summer)	42	2,923	This study
E. superba adult	60-78		Grantham (1977)
E. superba Juvenile (summer)	57	3,153	Färber-Lorda et al.
E. superba adult male (summer)	60	4,210	(2009)
E. superba adult (late spring)	41-50		Meyer et al. (2010)
E. superba adult (autumn)	29-52		
E. superba adult	75		Gigliotti et al. (2011)

[a]DW, dry weight; ind, individual.

The low nutritional content of *S. thompsoni* determined by Dubischar et al. (2012) and in this study, combined with the energetic expense required to heat an individual to a suitable metabolic temperature, illustrates *S. thompsoni* as a sort of Southern Ocean "low carb" food (for warm-blooded predators, at least). Projected changes in Southern Ocean habitat are predicted to favour *S. thompsoni* populations, and disadvantage *E. superba* populations (Constable et al. 2014, Piñones & Fedorov 2016). If the future Southern Ocean zooplankton assemblage experiences more frequent *S. thompsoni* dominance, this "low carb" food may become a more common Southern Ocean prey source. The consequences of such a shift are unclear. Until recently, the majority of Southern Ocean ecosystem models excluded salp-based trophic linkages. This exclusion has, in part, limited current understanding of the trophic role of *S. thompsoni* and its potential impact on ecosystem structure and function. Nevertheless, new data continue to demonstrate the capacity of *S. thompsoni* to dominate the Southern Ocean zooplankton community (Ono & Moteki 2013, Ross et al. 2014, Steinberg et al. 2015), and accurate representations of salp trophodynamics are now considered essential for high resolution ecosystem models (Murphy et al. 2012).

Due to the low proportion of primary production consumed by *S. thompsoni*, recent, comprehensive quantifications of Southern Ocean energy pathways have deemed *S. thompsoni* a "production loss" pathway (Ballerini et al. 2014). Extending on this low energy return, Rogers et al. (2012) claim that, although the salp energy pathway is complex, it is not capable of supporting higher-trophic-level biomass. Concerns surrounding flow-on effects of increased *S. thompsoni* production centre on how an *E. superba*-to-*S. thompsoni* prey shift may compromise ecosystem structure and function. This focus is understandable: the minimum daily energy requirement of a male Chinstrap penguin is 3,002,000 J (Croll & Tershy 1998), which, based on the energy content results of this study, can be satisfied by (at least) approximately 1,000 adult *E. superba*, or, over 100,000 *S. thompsoni*. Fig. 4.5 summarises the daily energetic needs of Chinstrap, Gentoo and Adelie penguins: three higher order predators that may be faced with *S. thompsoni* as an alternative food source when foraging for *E. superba*. Across the species, for a male or female to satisfy their daily metabolic needs, the number of *S. thompsoni* required (based on the energy content determined in this study) exceeds 100,000 individuals. Furthermore, what must also be considered is how increasing *S. thompsoni* abundances may alter the condition of warm-blooded higher trophic level predators with an existing copepod-based, or gelatinous-based diets. One of the most abundant Southern Ocean copepods, *Calanoides acutus*, is approximately 18% protein (DW) (Drits et al. 1994) and contains around ~400 J ind^{-1} (Clarke et al. 1992), greatly exceeding the energetic potential of a single *S. thompsoni*. It would also appear that not all gelatinous organisms are equal, as, while the hydrozoan, *Calycopsis borchgrevinki*, and the cnidarian, *Atolla wyvillei*, have an identical water content as *S. thompsoni* (95%), both are higher in nutritional value (*C. borchgrevinki* dry weight is 11% protein, and *A.*

wyvillei is 17% protein (Clarke et al. 1992)). Consequently, copepod, hydrozoan and cnidarian predators (in addition to typical *E. superba* predators) may be at an energetic loss during extended periods of increased *S. thompsoni* abundance and failure to acknowledge, and quantify, the effect of *S. thompsoni* blooms on jellyfish and copepod feeders may lead to an underestimation in predicted impacts on higher trophic level biomass. It must also be noted that increased *S. thompsoni* production may alter the regular predatory routes, and behaviour, of higher trophic level species, particularly through avoidance behaviour. Based on the responses of Gentoo and Chinstrap penguins, overlapping *E. superba* and *S. thompsoni* populations can be distinguished as two unique prey sources, with *S. thompsoni* rarely consumed (Kokubun et al. 2013). Hence, higher trophic level species not ingesting *S. thompsoni* may still experience an energetic loss through effort invested in active avoidance. The extent of this alternative energy expense requires substantial further research. Visual data, including output from predator-mounted cameras, will no doubt prove pivotal in clarifying behavioural responses in higher trophic level species.

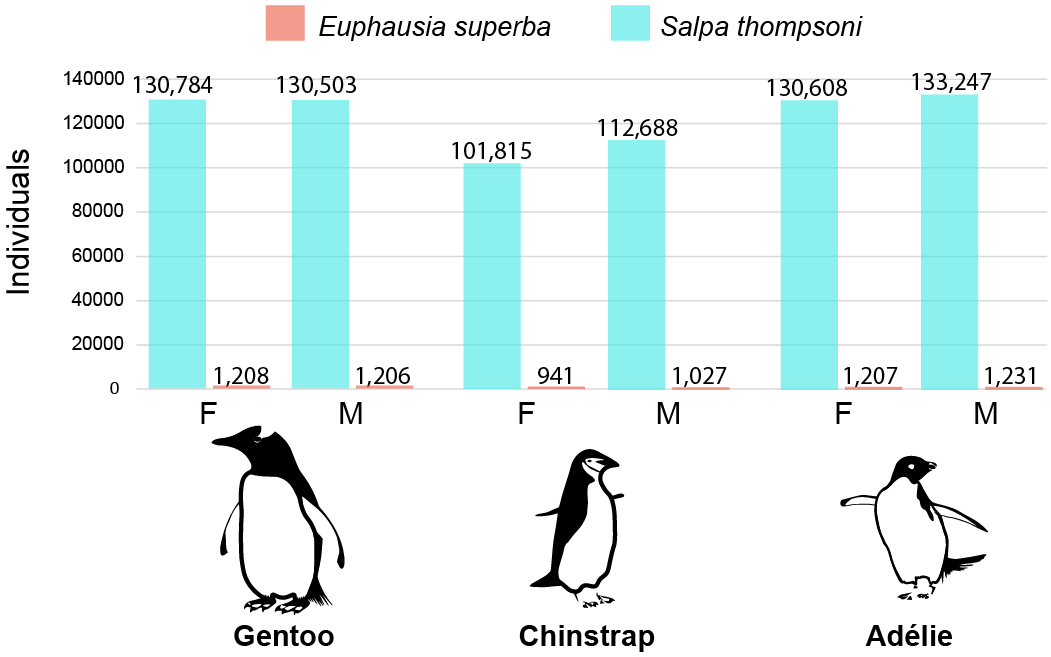


Figure 4.5 Number of individual *Salpa thompsoni* (left-hand, blue columns) and *Euphausia superba* (right-hand, red columns) required to satisfy the daily metabolic requirements (Croll & Tershy 1998) of female (F) and male (M) Gentoo, Chinstrap and Adelie penguins, based on the energetic profiles in this study.

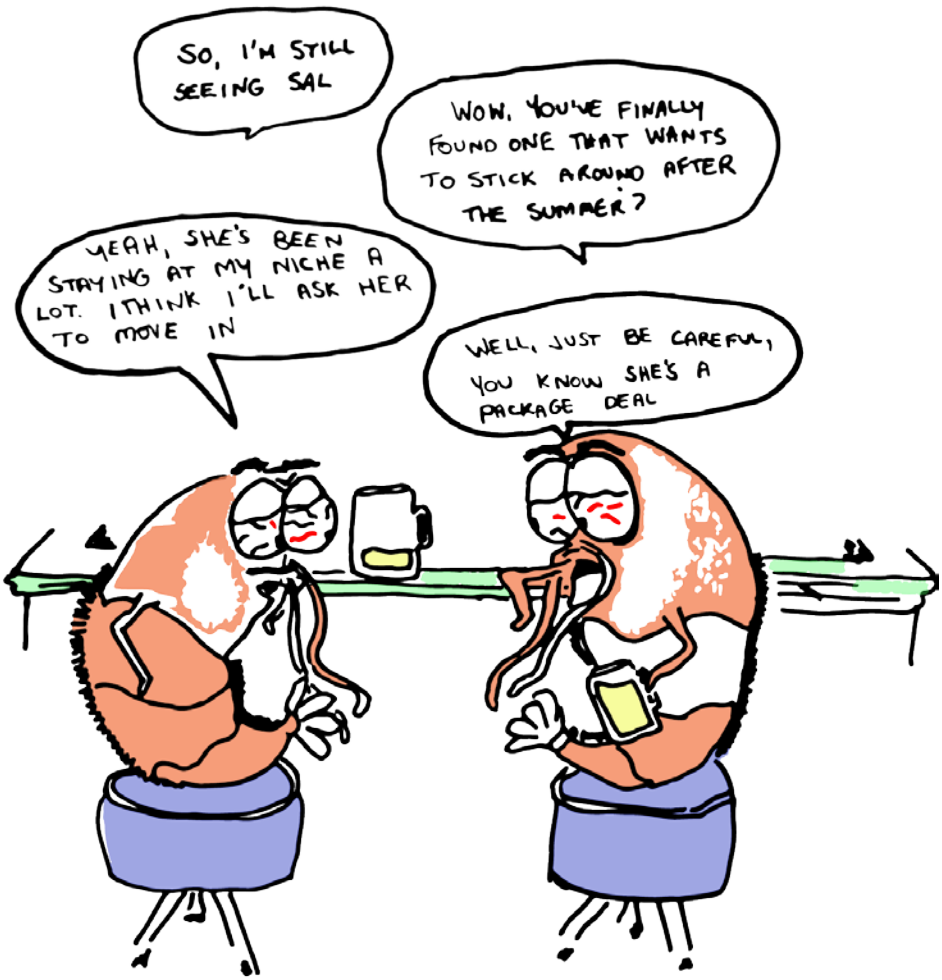
For any predator within an ecosystem, whether an item of prey is energetically favourable to consume will depend on three basic criteria: 1. Ease of capture, 2. Ease of metabolisation and 3. Raw nutritional content. As discussed, *S. thompsoni* aggregates are available as a bulk-food source, minimising effort required for capture. While future research will clarify the energetic trade-off involved in capturing and consuming *S. thompsoni*, it is reasonable to assume that the accessibility of aggregates might not compensate for the energetic expense of heating an individual to metabolising temperature, or for the relatively low protein and energy content. In summary, the results of this study, and earlier West Antarctic-based research, provide evidence that suggests that *S. thompsoni* may be an inadequate prey source for higher order species

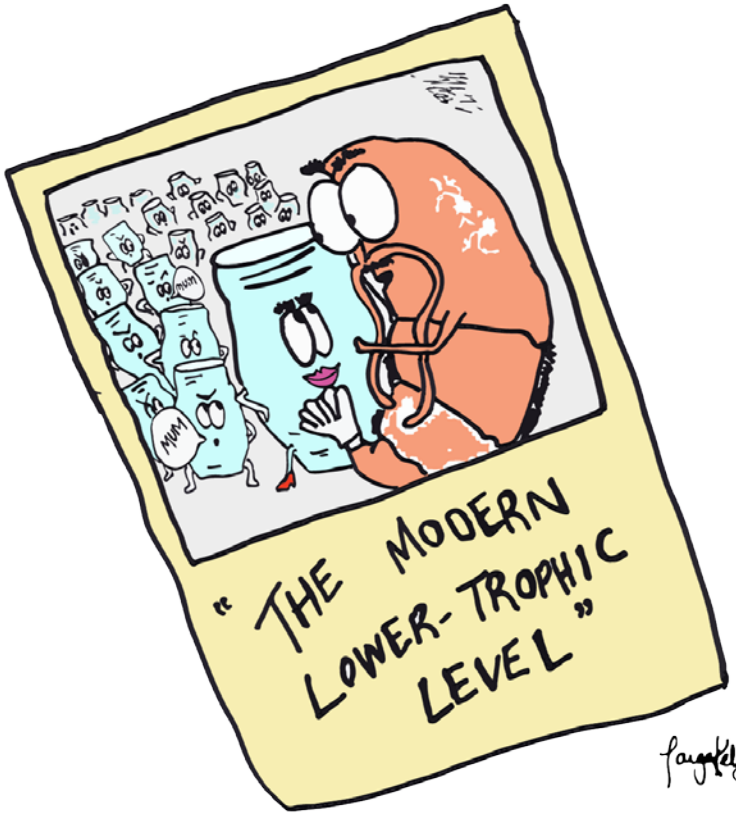
typically feeding on *E. superba*, copepods, and other gelatinous species. Furthermore, the consensus across the literature is that an increasingly prevalent *S. thompsoni* energy pathway will exert an overall negative ecosystem effect through reducing the amount of energy transferred from phytoplankton to higher order predators. However, at this stage, a lack of *in-situ* estimates of *S. thompsoni* trophodynamics are hindering quantifications of the ecosystem input from the species. It must again be mentioned that there is variation across the few existing literature estimates of *S. thompsoni*, and that unidentified proteins or glycoproteins can remain after biochemical analysis (Clarke et al. 1992, Dubischar et al. 2006), leading to an underestimation in protein content. Such methodological complications, however, are beyond the scope of this work, while repeated sampling across the Indian Sector is needed to clarify seasonal and individual-to-individual variation.

4.7 Conclusions

This study presents quantitative information on Indian Sector *S. thompsoni* morphometrics, elemental composition and nutritional value. In addition, this study also provides a direct, regionally and spatially explicit comparison of *S. thompsoni* and *E. superba* trophodynamics, something that is often difficult to achieve due to the unpredictable nature of *S. thompsoni* blooms. Evidence suggests that the traditional, *E. superba*-based Southern Ocean ecosystem structure is shifting towards a structure favouring alternative energy pathways, with increased *S. thompsoni* influence at lower trophic levels (Fig. 4.5). Furthermore, it is predicted that, under a high $C0_2$ emissions scenario (Intergovernmental Panel on Climate Change 2013), reductions in summer sea-ice extent and increases in sea-surface temperatures will drive a long term regime shift

in the Southern Ocean ecosystem where *S. thompsoni* replace *E. superba* (Rintoul et al. 2018). As *S. thompsoni* may become a permanent fixture in the future Southern Ocean ecosystem, it is essential that models accurately reflect the energetic consequences of both *S. thompsoni* consumption and avoidance. Data from this study provides a comprehensive assessment of *S. thompsoni* that will improve the parameterisation of East Antarctic ecosystem models estimating future energy flow in the Southern Ocean. This will, in turn, aid increasing confidence surrounding statements of ecosystem change in polar regions, which is currently limited due to a lack of data to estimate whether change has occurred (Nymand Larson et al. 2014, Constable et al. 2017).


SO, I'M STILL SEEING SAL
WOW, YOU'VE FINALLY FOUND ONE THAT WANTS TO STICK AROUND AFTER THE SUMMER?
YEAH, SHE'S BEEN STAYING AT MY NICHE A LOT. I THINK I'LL ASK HER TO MOVE IN
WELL, JUST BE CAREFUL, YOU KNOW SHE'S A PACKAGE DEAL


MUM
"THE MODERN LOWER-TROPHIC LEVEL"

CHAPTER 5

The ecosystem role of *Salpa thompsoni* in the Kerguelen Plateau region: discussion and conclusions

5.1 Gelatinous organisms in the modern ocean: fact vs. fiction

The apparent rise in gelatinous species is one aspect of global marine change that has captured the attention of both the scientific community and the general public. Based on the Scopus citation database, over 300 hundred peer-reviewed articles on gelatinous zooplankton have been published over the past decade[2]. In addition, mainstream media reports of harmful gelatinous species expanding their distribution patterns (primarily Irukandji jellyfish) are also now commonplace (Foster 2018). While there is undoubtedly a "hype" surrounding trends in gelatinous zooplankton, interpretations of findings are somewhat clouded by public misconceptions. Myths skewing common perception of the ecosystem role of gelatinous zooplankton are discussed at length by Condon et al. (2012), who stress that, while some abundance trends in these organisms can be associated with anthropogenic environmental change, they are not a new phenomenon in global oceans. It is thought that Ctenophora, the oldest gelatinous phylum, appeared around 540 million years ago (Chen et al. 2007), while pelagic tunicates entered marine ecosystems during the Neogene, 20-30 million years ago (Rigby & Milsom 2000). Subsequently, such gelatinous phyla and subphyla have, impressively, survived periods of abrupt environmental change that wiped out

[2] Result includes peer-reviewed journal articles published from 2008-2018, with "gelatinous zooplankton" listed in article title, abstract or keywords.

marine reptiles, ammonites and trilobites (Condon et al. 2012). Still, the knowledge that gelatinous organisms have "been here the whole time" is of little comfort to the scientific community and the public. In fact, this apparent resilience may be abetting the notion that the global oceans are undergoing a gelatinous zooplankton takeover. Furthermore, compared to marine mammals and fish, gelatinous zooplankton are grossly understudied (Richardson et al. 2009), with this longstanding lack of information no doubt fostering the sense of urgency in understanding how these jellylike organisms are responding to physical and chemical change.

There are also several complications associated with studying gelatinous zooplankton in the field, and these can make drawing concrete conclusions about the temporal and spatial patterns of gelatinous species difficult. To elaborate on this, discrete net hauls are common practice for gaining information on gelatinous blooms (e.g. bloom density), however, this method can provide only a snapshot of what are often spatially inconsistent aggregations with rapidly changing community structure. Consequently, net sampling does not always provide most accurate estimates of the size, biomass, distribution and movement of blooms (Schaub et al. 2018). Until recently, the trophic role of gelatinous species has also been difficult to estimate. Gelatinous organisms tend to rapidly deteriorate once consumed, and they often appear absent (or are in such poor condition they are unidentifiable) when the gut contents of a higher trophic level species are analysed (Arai et al. 2003). This, in turn, has led to biased diet assessments, with the gelatinous component of diets of potential predators, in particular, underestimated (Berry et al. 2015). Further, reducing our knowledge of gelatinous zooplankton is the global focus on jellyfish (Condon et al. 2013, Sanz-Martín et al. 2016). This focus has allowed other gelatinous phyla and subphyla (including

tunicate salps) to fly under the research radar. Undeniably, the long-term neglect of Thaliacean biology and ecology can partly be credited to genera such as *Salpa* not posing a direct threat to human health. Furthermore, tunicates are, generally, less abundant than cnidarians and ctenophores, and constitute only 2.5% of total global zooplankton biomass (Lucas et al. 2014). Still, by clogging fishing nets, and even power plant components (Sneed 2012, Boero et al. 2013), salp blooms can exert a major effect on economic returns and human quality of life.

Based on current knowledge, one of the major poorly-understood consequences of salp blooms is their overall ecosystem effect, particularly that in the Southern Ocean. Like jellyfish, Southern Ocean salps also receive media attention, with their potentially increasing abundances "spelling big trouble" for the Antarctic and Southern Ocean ecosystem (Carr 2017, Engelmann 2018). In some respects, the trophic structure of the Southern Ocean and Antarctic ecosystem is more fragile than many temperate regions, owing to a reliance on *Euphausia superba*: the primary food source for numerous higher trophic level species. What is crucial to remember, however, is that behind any labels bestowed by public media, published data (much of it sporadic) on the most abundant Southern Ocean salp, *Salpa thompsoni*, has only been available for the last fifty years. It is also imperative to approach Southern Ocean salp research with an open mind; not to solely seek out apparent increases in salp numbers, but to appreciate what abundance information might also reveal about population cycles and environmental drivers. Considering the evolutionary success of salps, and the potential for localized summer blooms to numerically exceed that of all other Southern Ocean zooplanktors in a region (Steinberg et al. 2015), our incomplete knowledge of *S. thompsoni* biology and ecology presents itself as a major hurdle in understanding fundamental trophodynamics in polar

regions. In turn, grey areas surrounding the knowledge of these transparent organisms may eventually hinder advancements in pro-active ecosystem-based policy.

Baseline information against which to quantify change in gelatinous zooplankton populations is necessary for eliminating the "perceptionalised bias" (where an observer establishes patterns based on occurrences from the immediate past only) that surrounds research into the long-term trends of species such as *S. thompsoni* (Condon et al. 2012). This multi-faceted thesis presents baseline information on *S. thompsoni* biology, trophodynamics and environmental responses in the ecologically significant, but understudied Kerguelen Plateau Region. The data and findings from this research will have applications for subsequent studies further deciphering *S. thompsoni* trophodynamics, as well as whole-of-ecosystem models. Along with providing new information on Southern Ocean salps, findings from this study will also add perspective to existing *S. thompsoni* knowledge. The impact of improved perspective, or sorting "fact from fiction" should not be underestimated, as common perceptions significantly influence (whether it be consciously or sub-consciously) how scientific research is conducted and communicated.

In summary, this thesis found that, within the Kerguelen Plateau Region:

- Discrete *S. thompsoni* blooms can exceed 2, 500 individuals 1,000 m^{-3}, which, compared to 1993-2009 West Antarctic density trends, is larger than most summer maxima (Loeb & Santora 2012).
- During summer 2016, the maximum *S. thompsoni* density (2,560 ind. 1,000 m^{-3}) was approximately 6x greater than the historical (1982-2008) maximum (603

ind. 1,000 m^{-3}) for this region. Maximum 2016 densities also occurred further south (63.29°S) than historical maxima (*circa* 60°S) in this region.

- Summer 2016 *S. thompsoni* bloom production was associated with lower chlorophyll-*a* (highest abundances occurred at stations where depth-integrated chlorophyll-*a* was <65 mg m^{-3}), late afternoon to twilight light conditions, and sea-ice retreat.
- January-February signifies a period of high *S. thompsoni* aggregate production, and preliminary solitary production, which is consistent with West Antarctic Peninsula accounts of life cycle (Loeb & Santora 2012).
- *Salpa thompsoni* aggregate carbon and nitrogen content is more variable, and lower, than Southern Ocean euphausiids (*Euphausia frigida*, *E. superba*, *Euphausia triacantha* and *Thysanoessa macrura*).
- Based on $\delta^{13}C$, $\delta^{15}N$ ratios, *S. thompsoni* is more similar to *E. superba* than to other Southern Ocean euphausiids (*E. frigida*, *E. triacantha* and *T. macrura*) in terms of trophic position.
- The diets of Kerguelen Plateau *S. thompsoni* and *E. superba* were shown to overlap through the shared consumption of diatoms in the genus *Fragilariopsis*.
- As a food source for higher trophic level species, *S. thompsoni* aggregates contain, on average, less than 100x the energy content (~27 Joules $ind.^{-3}$ vs. 2,900 Joules $ind.^{-3}$) and one sixth of the protein content (7% dry weight vs. 42% weight) of *Euphausia superba*.

In addition, this study found that, across the Indian Sector of the Southern Ocean:

- Based on 1981-2016 abundance data, the southern Kerguelen Plateau region is a potential hotspot for horizontal (latitudinal and longitudinal distribution), and vertical (water-column distribution) habitat overlap between *S. thompsoni* and *E. superba*.
- Based on historical (prior to 2016) density patterns, *S. thompsoni* has only been sampled during summers when latitudinal sea ice extent has not extended further north than 58.24°S.
- Over the last 35 years of sampling, the rate of trawls retrieving *S. thompsoni* that were aimed at an acoustic *E. superba* target has not decreased, highlighting the need for further investigation into salp "bycatch" in euphausiid targeted trawls.

5.2 Synthesis of findings

2016 Kerguelen Plateau Salpa thompsoni *density and distribution patterns*

This thesis presents 2016 summer *S. thompsoni* densities and distribution patterns for 40 locations in the southern Kerguelen Plateau region, representing the most comprehensive gelatinous zooplankton abundance dataset for the area. The ecosystem of the Kerguelen Plateau and the surrounding Indian Sector region is, generally, understudied in comparison with other regions, with methodologically comparable zooplankton density data collected only during 1985 (SIBEX II), 1987 (AAMBER), 1991 (AAMBER II), 1993 (KROCK), 1996 (BROKE) and 2006 (BROKE-West). While the maximum KAXIS *S. thompsoni* densities recorded in the present study exceed previous reports, the temporal sparseness and spatial inconsistency across historical sampling means that neither a long-term increasing trend, nor a long-term

southerly shift in populations can be confidently inferred. While identifying long-term abundance trajectories is pivotal for clarifying the changing ecosystem role of *S. thompsoni*, it is also crucial that research objectives do not solely centre on the hunt for abundance increases, and that the full extent of research outcomes are explored and appreciated. What the 2016 density and distribution patterns can confirm is that *S. thompsoni* in the Kerguelen Plateau region has the potential to occur in densities more than double the historical maxima, and that densities south of the Southern Antarctic Circumpolar Current Front are larger than suggested by historical studies. Across the historical East Antarctic studies, maximum *S. thompsoni* densities south of the Southern Boundary did not exceed 100 ind. 1,000 m^{-3}, while, during 2016 sampling, over 300 ind. 1,000 m^{-3} were sampled at 61.13°S. 2,520 ind. 1,000 m^{-3} were also sampled on the border of the Southern Boundary, at 64.41°S.

This thesis offers a much-needed, updated perspective regarding whether Indian Sector and West Antarctic *S. thompsoni* are occurring at a similar order of magnitude. Compared to long-term (1993-2009) West Antarctic trends, the largest KAXIS *S. thompsoni* bloom (2,560 ind. 1,000 m^{-3}) was large for a discrete group, exceeding bloom maxima during twelve of the seventeen summers sampled by Loeb and Santora (2012). Based on this regional comparison, the Kerguelen Plateau may be an underappreciated region of heightened *S. thompsoni* ecosystem importance. Salps have the potential to be a major shaper of future Southern Ocean ecosystem structure and function (McBride et al. 2014) and improved knowledge of abundances and distribution patterns of *S. thompsoni* at both circumpolar and regional scales is needed to improve the capacity of ecosystem models to reproduce

current tropho-dynamics, as well as provide more accurate predictions of future changes. This study provides a highly significant dataset for the southern Kerguelen Plateau, and Indian Sector, *S. thompsoni* bloom density and distribution, which will serve as an essential foundation in future salp time-series analyses, lower-trophic-level dynamics studies, and whole-of-ecosystem models.

2016 Kerguelen Plateau Salpa thompsoni community composition

The *S. thompsoni* life cycle is split into two life phases: aggregate (blastozooid) and solitary (oozoid). Typical aggregate regeneration time is estimated at ~ 7 weeks, with aggregate production (and overall abundances) peaking from November to March. Solitary regeneration time is estimated at 7.5 months, with production peaking from March-April (Loeb & Santora 2012). There is, however, evidence of trans-sector differences in *S. thompsoni* growth rates, with the potential for the entire life cycle (sexual + asexual phases) to complete within 2-3 months (Pakhomov & Hunt 2017). The potential for variability in fundamental *S. thompsoni* properties highlights the need for spatially explicit records of community assemblage and morphometrics. The KAXIS *S. thompsoni* community composition and morphometrics presented in this study is the most comprehensive of such data for *S. thompsoni* in the Kerguelen Plateau region. Across the KAXIS routine trawls, the overall community comprised 90% aggregates (approximately 72,000 individuals) and 10% solitaries (approximately 8,000 individuals). Within the aggregate community, most individuals were immature (39%) or developing (38%). Within the solitary subsample, most salps were developing (24%) or immature (18%), and both the KAXIS life stage assemblage and aggregate and solitary maturity stage distributions were consistent with previous reports of summer *S. thompsoni*

community composition (Pakhomov et al. 2011, Loeb & Santora 2012). Within an *S. thompsoni* population, the proportion of aggregates and solitaries will impact on the ecosystem role of the species. To illustrate this further, solitary salps are more protein-, nitrogen- and carbon-rich than aggregates (Dubischar et al. 2012), however, chain-forming aggregates are present as a more concentrated food source. Consequently, the appeal of *S. thompsoni* as a prey source, as well as its role in nutrient cycling, will shift with life stage composition. At present, studies on the potential for *S. thompsoni* to alter marine biogeochemistry (Alcaraz et al. 2014, Cabanes et al. 2017) are yet to analyse solitary individuals.

To determine *S. thompsoni* growth rates for the Kerguelen Plateau region, repeated sampling of a single population would have been optimal, though logistically not feasible. For that reason, in-*situ* growth rates have not been calculated for this study. Nonetheless, the KAXIS life and maturity stage data provide baseline seasonal cycle information for Kerguelen Plateau *S. thompsoni*, which is essential for elucidating the ecosystem input of a species with inconsistent and unpredictable distribution patterns.

Drivers of 2016 Kerguelen Plateau Salpa thompsoni *abundance patterns*

To gauge the potential impact of *S. thompsoni* on ecosystem processes such as energy flow, future population trajectories must be identified, and responses to predicted environmental change quantified. Despite evidence of an increasing ecosystem role relative to other major Southern Ocean zooplanktors (including *E. superba*) the environmental drivers of distribution trends in *S. thompsoni*, and even basic presence/absence patterns, are not well understood (Constable et al. 2014). In

part, this lack of understanding can be attributed to an imbalance in regional research effort, and subsequent knowledge of *S. thompsoni* population responses. Off the West Antarctic, several multi-decadal studies have documented *S. thompsoni* bloom behaviour, linking increased abundances with declining sea-ice extent (Atkinson et al. 2004, Steinberg et al. 2015), variation in the El Niño Southern Oscillation Index and the Southern Annular mode (Steinberg et al. 2015), and movement of warm Antarctic Circumpolar Current water (Ross et al. 2014). Conversely, *in-situ* Indian Sector studies have only observed populations over short time-scales (<2 months) (Nicol et al. 2000b, Ono & Moteki 2013, 2017), and environmental/abundance linkages have not always been attempted. BROKE, one of the few East Antarctic surveys to identify potential bloom triggers, associated increased (1996) summer *S. thompsoni* abundances with decreased sea ice extent, warmer temperatures and lower chlorophyll-*a* (Nicol et al. 2000b). These findings, however, were based on correlational conclusions.

The present study is the first to establish *S. thompsoni* bloom drivers through statistical modelling methods for the southern Kerguelen Plateau region. Using Generalised Additive Models, this study identified low chlorophyll-*a*, late-afternoon to twilight light conditions and declining latitudinal sea-ice (eight weeks post initial sea-ice retreat is optimal) as drivers of increased *S. thompsoni* abundance across the Kerguelen Plateau region. The relationships identified in this work are in line with the preliminary observations of the BROKE survey, validating the role of sea-ice extent and primary production in the distribution patterns of *S. thompsoni* in East Antarctica. The results of this study do not discount the role of temperature and large-scale climate forces (highlighted as major drivers in West Antarctic *S.*

thompsoni populations), and instead, may highlight east-west differences in population responses to temperature and sea-ice. On a circumpolar scale, the future Southern Ocean is predicted to experience a poleward migration of warm, deep water, as well as a reduction in summer sea-ice extent (Stocker 2014). This thesis provides an essential foundation for future quantitative research into estimating Indian Sector salp biomass and ecosystem input alongside such physical and chemical changes.

The relationship between Salpa thompsoni *and euphausiids in the Kerguelen Plateau: the potential for habitat and food source partitioning*

In media reports, much of the appeal of any "salp story" lies in the potential for *S. thompsoni* to threaten *E. superba* populations, whether it be through competition for food, or for habitat. In the literature, however, studies researching the potential for *S. thompsoni* and *E. superba* habitat partitioning have returned mixed results. While spatial (Hosie et al. 2000, Pakhomov et al. 2002, Pakhomov 2004) and temporal (Ross et al. 2014, Steinberg et al. 2015) segregation between *S. thompsoni* and *E. superba* populations is typical, there is evidence of West Antarctic broad-scale habitat (Ross et al. 2014) and food source overlap (Loeb et al. 1997). This spatial and dietary overlap, together with trends suggesting that *S. thompsoni* populations are encroaching on traditional *E. superba* habitat (Atkinson et al. 2004, Ross et al. 2014), calls for a re-evaluation—or, in the case of the Kerguelen Plateau region, an evaluation—of *S. thompsoni*/*E. superba* resource partitioning. This thesis identified the southern Kerguelen Plateau as a potential East Antarctic region of both horizontal (latitudinal and longitudinal distribution) and vertical (water column distribution) habitat overlap, as well as dietary overlap, in *S. thompsoni* and *E.*

superba. Based on gut content and stable isotope analysis, the diet and trophic position of *S. thompsoni* was more like that of *E. superba* than that of other Southern Ocean euphausiids (*E. frigida*, *E. triacantha* and *Thysanoessa macrura*). These results highlight *E. superba* as a species that is potentially more susceptible to salp-associated pressures than other euphausiids. Furthermore, this study identified *Fragilariopsis* diatoms as a major source of dietary overlap. Consequently, the distribution patterns of *Fragilariopsis* diatoms may be an underacknowledged biological driver of *S. thompsoni*/*E. superba* overlap, and any long-term competition for this phytoplankton may have consequences for *E. superba* populations.

While future, repeated assessments of resource partitioning on varying spatial and temporal scales are clearly needed, the results of this study provide evidence that Kerguelen Plateau *S. thompsoni* blooms are a potential competitive pressure on *E. superba* populations. This work also raises the question of whether *S. thompsoni* blooms might impact on *E. superba* sampling efficiency, particularly through hindering the effectiveness of *E. superba* targeted trawls. Further research into salp "bycatch" in euphausiid-targeted trawls could have financial and operational benefits for both science and industry.

Salpa thompsoni *and* Euphausia superba *elemental and energetic profiling: could a "sometimes food" become a "staple food?"*

Euphausia superba is the staple food source of the Southern Ocean and is consumed by fish, squid, whales, seals and penguins. Because of this pivotal role in energy transfer, *E. superba* is considered a "keystone species," meaning it has a central role in ecosystem structure and function. Long-term trends in West Antarctic zooplankton (Atkinson et al. 2004, Steinberg et al. 2015), however, suggest that *S.*

thompsoni can, at least in terms of biomass, replace *E. superba*. Irrespective of whether *S. thompsoni* blooms dominate the zooplankton community on a short-term or a long-term basis, heightened production will increase the availability of *S. thompsoni* as a food source for typical *E. superba* predators, changing the Southern Ocean "menu."

In early estimates of energetic potential, *S. thompsoni* was considered a "trophic dead end" (Verity & Smetacek 1996). (The slightly more flattering term of trophic "cul-de-sac" has also been applied (Lee et al. 2010)). Advances in dietary analysis, however, have revealed *S. thompsoni* to be ingested (whether intentionally or unintentionally) by Antarctic fish and seabirds (Yves et al. 2002, Raga et al. 2015). The effect of extensive *S. thompsoni* consumption on the condition and behaviour of typical *E. superba* predators is unclear, with limited studies investigating the metabolic return of *S. thompsoni* (Ikeda & Bruce 1986, Reinke 1987, Huntley et al. 1989, Dubischar et al. 2012). Considering the potential spatial variation in fundamental *S. thompsoni* parameters (e.g. growth rates (Pakhomov & Hunt 2017)), regionally explicit reports of biochemical properties are needed to inform more accurate estimates of *S. thompsoni* energetic value.

This thesis presents the first elemental (carbon and nitrogen) and energetic (including protein) profile of Kerguelen Plateau *S. thompsoni*, and the first elemental and energetic profile for Indian Sector *S. thompsoni* for 30 years. On average, carbon, nitrogen and protein accounted for 18%, 4% and 7% of *S. thompsoni* dry weight, respectively, and an individual contained 27 J. When evaluating the changing ecosystem role of salps, Henschke et al. (2016) described *S. thompsoni* as having a "high" protein content. In the most meaningful sense, for a Southern Ocean zooplanktor to be deemed "high" in any nutritional property, the nutritional content should first be compared with

that of a benchmark food source; e.g. *E. superba*. We also analysed KAXIS *E. superba* for protein and energy content, finding adult individuals to contain more than six times the protein (% dry weight), and more than 100 times the energy, of aggregate *S. thompsoni*. Consequently, this study considers *S. thompsoni* to be an energy-poor food source for typical *E. superba* predators. While some predators of *S. thompsoni* (most notably seabirds), will be capable of extracting select body parts for consumption, evidence of whole salps in the stomach contents of shy albatrosses (Hedd & Gales 2001), as well as a combination of salp muscle bands and guts the stomach contents of Atlantic butterfish (Mianzan et al. 1996), suggests that consumption of whole individuals is common practice.

The potential nutritional value of *S. thompsoni* will be further reduced by the energetic investment required to heat an individual (which is ~96% water) to metabolic temperature. While all food needs to be heated to metabolic temperature after consumption, a predator would need to invest more energy in heating *S. thompsoni* than it would in heating euphausiids such as *E. superba* or *T. macrura*, which are both approximately 80% water (Mizdalski 1988). To place the nutritional content results of this study into a "real life" feeding scenario, a female Kerguelen Pleateau Adelie penguin with a daily energetic requirement of 3.53 MJ (Croll & Tershy 1998) could be metabolically satisfied with approximately 1,200 adult *E. superba*, but would need approximately 130,600 aggregate *S. thompsoni*. (Whether an Adelie penguin's stomach can hold 130, 600 *S. thompsoni* is a question in itself.) While further research is required to identify the response of *E. superba*-predators to *S. thompsoni* blooms, as well as understanding *S. thompsoni* digestibility, this work provides evidence that, in agreement with Murphy et al. (2016), a phytoplankton-salp-higher order predator trophic pathway

is energetically inadequate. The elemental and nutritional datasets from this work will serve as input into regionalised studies aiming to quantify the energy lost via this alternative trophic pathway.

5.3 Research applications and future directions

This work provides a series of temporally and spatially comparable datasets on fundamental, yet under-researched aspects of *S. thompsoni* biology and ecology. These datasets encompass *S. thompsoni* density (abundance) and distribution patterns, morphometrics, environment/density relationships, elemental composition and energetic content. Also, several of these datasets are either the first of such information or at least the first for more than 30 years, for salps in the Indian Sector of the Southern Ocean. This new information will have several applications for future research, including studies further investigating the prey potential of *S. thompsoni*, and parameterization of whole-ecosystem models aiming to quantify changing ecosystem energy flow.

Ecosystem models

A potential immediate application for these data will be in parameterising Kerguelen Plateau ecosystem models. The Kerguelen Plateau is being increasingly recognised as a unique geographic region, significant for its wind-driven upwelling events (Gille et al. 2014) and subsequent biological productivity (Arrigo et al. 2008, Duhamel & Welsford 2011, Bestley et al. 2018). Two symposia on Kerguelen Plateau Marine Ecosystem and Fisheries have been held (2010, 2018), with major themes including changes in key food web components (including salp abundances) (Mayzaud et al. 2011), changes in energy transfer to higher trophic levels (Hunt et al. 2011), and how the precautionary management approach of the Commission for the Conservation of

Antarctic Marine Living Resources can be developed to adjust catch limits under climate change scenarios or other ecosystem pressures (Constable & Welsford 2011). Increased *S. thompsoni* production may be a valid biological pressure for the future Kerguelen Plateau ecosystem, and, to adapt management strategies to such changes, *S. thompsoni* must be adequately represented in ecosystem models.

Currently, many eastern Southern Ocean and Subantarctic Island ecosystem models classify salps as "other zooplankton," (e.g. Gurney et al. 2014), cloaking their ecosystem input within a combined estimate of miscellaneous zooplankton. "Other zooplankton" model classifications often comprise under-researched, but ecologically significant taxa, such as pteropods (a food source for larger zooplankton and whales (Hunt et al. 2008)). The Intergovernmental Panel on Climate Change (IPCC) recognise *S. thompsoni*/*E. superba* population interplay as a biological dynamic with extensive ecosystem effects (Intergovernmental Panel on Climate Change 2007), however, to comprehend and quantify future lower-trophic level change in ecologically and economically valuable regions such as the Kerguelen Plateau, researchers must tease out the ecosystem input of this "other zooplankton" group.

To represent the ecosystem input of *S. thompsoni* in mass-balanced Kerguelen Plateau models currently under development, information on mortality, consumption, biomass, and growth would be optimal (Subramaniam et al., under review). Recently, Henschke et al. (2018) developed a West Antarctic *S. thompsoni* population model with estimates of assimilation efficiency, growth rates, mortality rates and respiration rates. Until further, regionalised population-cycle models are developed, it is reasonable to apply the parameter evaluations of this model to East Antarctic populations. Together

with the population-cycle information in Henschke et al. (2018), the *S. thompsoni* bloom size and structure data in this thesis can satisfy the information requirements for a discrete *S. thompsoni* functional group in Kerguelen Plateau, and broader East Antarctic, models. Already, the data from this study have served as input into an Ecopath model representing the Prydz Bay ecosystem (McCormack et al. 2017). Other possible applications within the Ecopath with Ecosim modelling platform include exploring the impact of varying *S. thompsoni* abundance scenarios on both *E. superba* and typical predator populations of *E. superba*, as well as evaluating *S. thompsoni* prevalence in the Kerguelen Plateau region under predicted climate change scenarios.

Additional models that could utilise the *S. thompsoni* data collected as part of this research include those that are part of the MESOPP (Mesopelagic Southern Ocean Prey and Predators) project (MESOPP 2018). These models include Atlantis (Fulton et al. 2004, 2011) and MIZER (Blanchard et al. 2014, Scott et al. 2014, Blanchard et al. 2017) configurations for East Antarctica. Furthermore, if commercial *E. superba* fishing expands into the Indian Sector, mass-balanced models representing trophic interactions in specific fishing areas (as per the CCAMLR Sub-area 48.1 model (Cornejo-Donoso & Antezana 2008)) may also incorporate data from this research into their functional group estimates.

Future research into the potential of Salpa thompsoni *as a food source*

Improved dietary-analysis methods are continually revealing new predators of *S. thompsoni* (Raga et al. 2015, Henschke et al. 2018). There is, however, little information on how *S. thompsoni* blooms can affect the behaviour of higher order predators that typically feed on *E. superba*. There is evidence of *S. thompsoni* avoidance by Gentoo and

Chinstrap penguins (Kokubun et al. 2013), however, repeated behaviour patterns under multiple foraging conditions must be observed before a salp-bloom response can be determined. If typical *E. superba* predators (in this thesis also considered potential salp predators due to pelagic feeding) do utilise *S. thompsoni* as a prey source during periods of increased *S. thompsoni* production, the energy obtained through consumption will not only depend on nutritional content, but the size spectra of the *S. thompsoni* community, and the energy budget and prey handling behaviours of the prospective predator. During peak aggregate production, thousands of individuals may be present in a cubic meter and *S. thompsoni* accessibility is unlikely to be an issue for a prospective predator. Consequently, during "salp years" of reduced *E. superba* abundance, availability of *E. superba*-alternative prey may not be a key factor restricting energy flow. What is more probable to result in a reduced energy flow within a salp-based trophic pathway is the capacity of a typical euphausiid predator to consume and digest a meal that is potentially hundreds of times greater in volume than their usual *E. superba* feed. In future works, the comprehensive *S. thompsoni* morphometrics and nutritional content datasets from this research can be paired with the energy budgets and prey handling mechanisms of potential predators, answering the question, "will a typical *E. superba* predator be satiated with *S. thompsoni* before its metabolic needs are met?"

5.4 The trophic role of *Salpa thompsoni*: Future research needs, and conclusions

Recent syntheses of *S. thompsoni* information have added new perspective to existing knowledge (Schaafsma et al. 2018), however, to continue advancing our understanding of this species, and that of the changing Southern Ocean ecosystem, more in-*situ* data on fundamental *S. thompsoni* properties (particularly bloom

formation, 3D distribution of blooms, biochemical properties and trophic role) from understudied areas such as the Indian Sector of the Southern Ocean are needed. Multiple East Antarctic studies have bypassed reporting information on such fundamental *S. thompsoni* properties, due to a focus on *S. thompsoni*/*E. superba* interactions (Kawaguchi & Takahashi 1996, Nicol et al. 2000b, Rathod 2005). While it can be argued that these salp dynamics are outside of the scope of such studies, the potential impact of increasing *S. thompsoni* production on *E. superba* populations and ecosystem energy flow cannot be confidently predicted until we adequately understand what underpins *S. thompsoni* bloom formation, peak production, and demise. It is crucial that, in future studies coupling *S. thompsoni*/*E. superba* study aims, researchers collect and report data on *S. thompsoni* population basics. This will not only add valuable perspective to their own results, but aid in constructing an information series on fundamental Southern Ocean salp properties. This thesis provides foundations for such an information series, and, through the provision of several baseline datasets on Kerguelen Plateau *S. thompsoni* (covering distribution patterns and abundance; population life stage, maturity stage and size composition; stable isotopic ratios; and elemental and nutritional composition), will aid in elucidating the biology and ecology of a species that, despite having a potentially profound effect on the Southern Ocean ecosystem, has long been both poorly understood, and misunderstood.

APPENDICES

A1

Tables for Chapter 2: KAXIS routine and target trawl register, historical routine trawl register, and supplementary information for statistical tests

Table A1.1 KAXIS *Salpa thompsoni* routine trawls register[a,b,c]

Trawl	Date/Time (UTC)	Lat (°)	Lon (°)	Ind.	Abund. (ind. m^{-2})	Light cond.	Life stage
R000*	2016-01-22T07:31:18	-65.455	93.180	3	1	day	A=3
R01	2016-01-23T04:56:17	-63.473	93.551	0	0	day	
R02	2016-01-23T17:24:24	-62.998	93.590	63	2	dusk	
R03*	2016-01-24T07:44:31	-61.718	93.327	1,500	30	day	A=1,313 S=188
R04	2016-01-24T18:43:00	-61.134	93.562	2,250	76	dusk	
R05*	2016-01-25T07:16:47	-61.976	92.536	49	2	day	A=49
R06	2016-01-26T00:42:47	-62.303	91.520	3,125	46	day	
R07	2016-01-26T18:24:35	-62.393	89.659	6	1	dusk	
R08*	2016-01-27T07:44:28	-62.470	87.158	2,764	61	day	A=2,686 S=79
R09	2016-01-27T20:07:33	-62.482	85.887	2,588	64	dusk	A=2,588
R10*	2016-01-28T07:21:12	-62.530	83.905	18	1	day	A=18
R11	2016-01-28T23:57:57	-62.529	81.949	625	123	dusk	
R12*	2016-01-29T20:20:58	-63.292	82.042	7,313	511	dusk	A=2,436 S=4,878
R13*	2016-01-20T11:08:06	-63.930	83.065	20,000	450	day	A=20,000
R14	2016-01-31T09:48:09	-64.345	83.633	7,125	365	day	
R15*	2016-02-01T05:30:30	-64.410	84.769	11,875	504	day	A=11,875

R16	2016-02-01T22:32:10	-65.172	85.330	0	0	dusk	
R18*	2016-02-02T21:50:00	-65.042	91.494	3	1	dusk	A=3
R19	2016-02-03T14:12:50	-64.318	89.841	0	0	dusk	
R20	2016-02-04T01:14:20	-63.607	90.317	0	0	day	
R21	2016-02-04T15:43:09	-63.133	87.259	4	1	dusk	
R22	2016-02-04T22:16:00	-62.502	86.128	529	13	dusk	
R23*	2016-02-05T11:23:00	-61.936	85.035	8,750	117	day	A=7,500 S=1,250
R24	2016-02-06T00:31:00	-61.222	83.863	313	5	day	
R25	2016-02-06T13:27:42	-60.362	82.496	0	0	dusk	
R26*	2016-02-07T09:14:51	-59.344	81.073	3	1	day	A=3
R27	2016-02-07T21:33:00	-58.648	80.160	2	1	dusk	
R28*	2016-02-08T10:19:07	-58.223	81.912	113	3	day	A=113
R29	2016-02-08T21:47:00	-57.930	83.353	825	22	dusk	
R30*	2016-02-09T10:05:07	-57.608	84.608	50	1	day	A=50
R31*	2016-02-09T10:01:54	-57.838	85.290	750	16	day	A=663, S=88
R32*	2016-02-10T07:57:34	-58.875	85.141	14	1	day	A=14
R34*	2016-02-10T16:21:14	-59.101	84.411	750	17	dusk	A=675 S=75
R35	2016-02-11T10:34:10	-60.027	86.751	0	0	day	
R36	2016-02-11T23:54:00	-60.052	85.833	63	3	dusk	
R37	2016-02-12T13:41:37	-60.319	83.580	0	0	dusk	
R38*	2016-02-13T15:03:58	-60.910	79.882	1,585	26	dusk	A=1,585
R39	2016-02-14T08:26:31	-61.317	77.592	13	1	day	S=13
R40*	2016-02-15T01:28:00	-61.846	74.115	900	13	day	A=779 S=122
R42*	2016-02-15T10:46:59	-62.704	73.314	6,064	57	day	A=6,064

[a]Asterix after trawl number indicates morphometrics station. Sometimes, numbers of solitaries and aggregates were noted at non-morphometrics stations.

[b]Ind., individuals in trawl; light cond., light conditions; A, aggregates; S, solitaries.

[c]Densities are also reported in individuals m^{-2} for ease of comparison with other studies in the literature. To convert to individuals m^{-3}, divide abundances m^{-2} by 200 (metres trawl depth).

Table A1.2 KAXIS *Salpa thompsoni* target trawl register[a,b].

Trawl	Date/Time (UTC)	Lat (°)	Lon (°)	Ind.	Abund. (ind. m^{-2})	Depth (m)	Light cond.	Life stage
T01	2016-01-23T10:46:29	-63.472	93.557	0	0	12	Day	
T02	2016-01-23T13:19:56	-63.647	93.562	0	0	30	Day	
T03	2016-01-24T03:43:00	-61.883	93.300	5,938	19	10	Day	
T04	2016-01-25T08:42:39	-62.018	92.439	14	1	9	Day	A=14
T05	2016-01-25T09:32:43	-62.019	92.442	11	1	20	Day	
T06	2016-01-26T19:40:38	-62.393	89.662	22	1	1	Dusk	A=22
T07	2016-01-28T01:24:06	-62.520	84.070	1	1	1	Day	
T08	2016-01-28T08:01:19	-62.532	83.882	24	1	15	Day	A=24
T09	2016-01-28T09:28:01	-62.527	83.566	15	1	22	Day	A=15
T10	2016-01-31T10:20:27	-64.301	83.734	1,250	7	10	Day	
T11	2016-01-31T11:10:14	-64.266	83.839	0	0	10	Day	
T12	2016-01-31T12:03:00	-64.263	83.850	2,589	3	1	Day	
T13	2016-02-01T06:06:49	-64.421	84.786	1,188	11	15	Day	A=1,176 S=12
T14	2016-02-01T23:55:17	-65.166	85.769	1	1	25	Dusk	
T15	2016-02-03T14:48:00	-64.337	89.995	0	0	1	Dusk	
T16	2016-02-03T17:38:56	-63.987	89.124	0	0	1	Dusk	
T17	2016-02-04T23:26:00	-62.431	86.042	375	1	20	Dusk	
T18	2016-02-06T14:00:53	-60.355	82.463	0	0	30	Dusk	
T19	2016-02-06T15:43:19	-60.213	82.263	0	0	150	Dusk	

T20	2016-02-06T18:30:00	-60.213	81.887	0	0	1	Dusk	
T21	2016-02-08T09:43:58	-58.226	81.955	5	1	40	Day	A=5
T22	2016-02-09T23:00:00	-58.380	85.305	5	1	1	Dusk	
T23	2016-01-10T07:23:02	-58.873	85.142	0	0	25	Day	
T24	2016-01-11T10:25:34	-60.025	86.766	2	1	20	Day	
T25	2016-02-12T04:34:00	-60.180	84.732	1,875	1	5	Day	A=1,875
T26	2016-02-12T12:41:14	-60.323	83.565	0	0	50	Dusk	
T27	2016-02-14T06:39:41	-61.292	77.616	1	1	25	Day	
T28	2016-02-14T07:11:10	-61.285	77.616	0	0	1	Day	
T29	2016-02-14T07:29:16	-61.288	77.624	0	0	10	Day	
T30	2016-02-15T14:49:38	-63.420	72.654	7	1	15	Dusk	
T31	2016-02-18T06:25:00	-66.578	62.688	8	1	50	Day	
T32	2016-02-18T08:47:00	-66.505	62.881	0	0	15	Day	
T33	2016-02-18T16:31:18	-66.714	63.081	0	0	10	Dusk	
T34	2016-02-18T17:51:26	-66.711	63.302	0	0	15	Dusk	
T35	2016-02-18T18:24:00	-66.725	63.293	0	0	20	Dusk	
T36	2016-02-18T19:10:53	-66.711	63.320	0	0	5	Night	
T37	2016-02-18T23:56:00	-66.197	63.702	0	0	15	Dusk	
T38	2016-02-19T04:22:00	-66.066	63.520	0	0	5	Day	
T39	2016-02-19T07:27:35	-66.813	63.709	0	0	15	Day	
T40	2016-02-19T11:27:08	-66.179	63.928	0	0	10	Day	

[a]Ind., individuals in trawl; light cond., light conditions; A, aggregates; S, solitaries.

[b]Densities are also reported in individuals m^{-2} for ease of comparison with other studies in the literature. To convert to individuals m^{-3}, divide abundances m^{-2} by Depth (m).

Table A1.3 Historical (1982-2006) routine trawls in the Kerguelen Plateau area[a]

Survey	Date/Time (UTC)	Lat (°)	Lon (°)	Abund. (ind. m^{-2})	Density (ind. m^{-3})
SIBEX2	1985-01-15	-66.015	72.912	1	1
SIBEX2	1985-01-14	-67.997	72.957	0	0
SIBEX2	1985-01-15	-64.997	72.970	1	1
SIBEX2	1985-01-14	-67.022	72.985	0	0
SIBEX2	1985-01-16	-64.005	73.002	2	1
SIBEX2	1985-01-16	-62.997	73.003	1	1
SIBEX2	1985-01-20	-66.558	77.940	1	1
SIBEX2	1985-01-19	-64.000	77.970	3	1
SIBEX2	1985-01-18	-62.033	77.973	10	1
SIBEX2	1985-01-19	-65.018	77.987	1	1
SIBEX2	1985-01-20	-66.010	77.987	1	1
SIBEX2	1985-01-19	-63.007	77.995	1	1
SIBEX2	1985-01-13	-68.003	78.013	0	0
SIBEX2	1985-01-23	-60.002	82.982	39	1
SIBEX2	1985-01-22	-62.992	82.997	2	1
SIBEX2	1985-01-22	-61.988	83.003	1	1
SIBEX2	1985-01-21	-63.998	83.005	1	1
SIBEX2	1985-01-22	-60.995	83.008	42	1
SIBEX2	1985-01-21	-64.995	83.035	1	1
SIBEX2	1985-01-21	-65.287	83.038	1	1
SIBEX2	1985-01-25	-64.968	87.968	0	0
SIBEX2	1985-01-24	-62.000	87.978	1	1
SIBEX2	1985-01-24	-62.998	87.997	1	1
SIBEX2	1985-01-23	-60.997	88.007	26	1
SIBEX2	1985-01-24	-64.007	88.008	2	1
SIBEX2	1985-01-23	-60.003	88.022	143	1
SIBEX2	1985-01-26	-63.988	92.973	1	1
SIBEX2	1985-01-26	-61.997	93.002	28	1
SIBEX2	1985-01-26	-62.990	93.013	0	0
AAMBER1	1987-03-15	-65.170	72.923	1	1
AAMBER1	1987-03-19	-64.340	72.960	0	0
AAMBER1	1987-03-18	-62.660	72.978	27	1
AAMBER1	1987-03-19	-64.357	72.980	0	0
AAMBER1	1987-03-19	-66.010	72.980	0	0
AAMBER1	1987-03-17	-61.837	73.003	0	0
AAMBER1	1987-03-19	-63.493	73.003	1	1
AAMBER1	1987-03-08	-66.838	77.935	1	1
AAMBER1	1987-03-20	-65.167	77.967	0	0
AAMBER1	1987-03-17	-61.835	77.968	38	1
AAMBER1	1987-03-16	-62.665	77.977	9	1
AAMBER1	1987-03-20	-66.000	77.987	0	0
AAMBER1	1987-03-16	-63.508	77.995	1	1

AAMBER1	1987-03-16	-64.335	77.997	0	0
AAMBER1	1987-03-07	-68.010	78.032	1	1
AAMBER1	1987-03-21	-65.060	82.715	1	1
AAMBER1	1987-03-21	-64.327	82.967	0	0
AAMBER1	1987-03-22	-61.817	87.922	1	1
AAMBER1	1987-03-23	-64.363	87.965	0	0
AAMBER1	1987-03-23	-63.503	87.967	0	0
AAMBER1	1987-03-23	-62.662	87.973	1	1
AAMBER1	1987-03-23	-64.950	87.983	1	1
AAMBER2	1991-02-06	-68.507	70.497	0	0
AAMBER2	1991-02-09	-65.988	70.497	0	0
AAMBER2	1991-02-09	-65.009	70.501	0	0
AAMBER2	1991-02-09	-66.502	70.510	0	0
AAMBER2	1991-02-09	-65.498	70.525	0	0
AAMBER2	1991-02-07	-67.459	70.998	0	0
AAMBER2	1991-02-07	-67.896	71.086	0	0
AAMBER2	1991-02-08	-66.981	71.128	0	0
AAMBER2	1991-01-23	-65.497	71.993	0	0
AAMBER2	1991-01-22	-66.488	71.998	0	0
AAMBER2	1991-01-21	-67.503	71.999	0	0
AAMBER2	1991-01-21	-67.033	72.005	0	0
AAMBER2	1991-01-20	-68.019	72.011	0	0
AAMBER2	1991-01-23	-65.032	72.019	0	0
AAMBER2	1991-01-21	-66.046	72.070	0	0
AAMBER2	1991-01-19	-68.398	72.175	0	0
AAMBER2	1991-01-25	-67.476	73.490	0	0
AAMBER2	1991-01-24	-66.494	73.491	0	0
AAMBER2	1991-01-24	-65.515	73.495	0	0
AAMBER2	1991-01-24	-66.998	73.498	0	0
AAMBER2	1991-01-25	-68.001	73.502	0	0
AAMBER2	1991-01-24	-64.998	73.511	0	0
AAMBER2	1991-01-24	-66.000	73.516	0	0
AAMBER2	1991-01-26	-68.560	73.524	0	0
AAMBER2	1991-01-26	-69.000	74.263	0	0
AAMBER2	1991-01-29	-66.555	74.878	0	0
AAMBER2	1991-01-27	-68.516	74.933	0	0
AAMBER2	1991-01-27	-67.975	74.987	0	0
AAMBER2	1991-01-28	-67.016	74.990	0	0
AAMBER2	1991-01-29	-65.990	75.006	0	0
AAMBER2	1991-01-30	-65.007	75.018	0	0
AAMBER2	1991-01-29	-65.522	75.026	0	0
AAMBER2	1991-01-28	-67.478	75.034	0	0

AAMBER2	1991-02-02	-68.491	76.466	0	0
AAMBER2	1991-02-03	-68.946	76.482	0	0
AAMBER2	1991-01-30	-64.992	76.495	0	0
AAMBER2	1991-01-31	-66.998	76.503	0	0
AAMBER2	1991-01-31	-66.008	76.504	0	0
AAMBER2	1991-01-31	-66.506	76.505	0	0
AAMBER2	1991-01-31	-65.509	76.509	0	0
AAMBER2	1991-02-01	-67.533	76.550	0	0
AAMBER2	1991-02-01	-68.002	76.596	0	0
AAMBER2	1991-02-03	-68.524	77.419	0	0
AAMBER2	1991-02-03	-68.029	77.968	0	0
AAMBER2	1991-02-05	-65.004	77.978	0	0
AAMBER2	1991-02-05	-65.988	77.980	0	0
AAMBER2	1991-02-05	-65.498	77.984	0	0
AAMBER2	1991-02-04	-66.508	78.001	0	0
AAMBER2	1991-02-04	-66.996	78.001	0	0
AAMBER2	1991-02-04	-64.169	83.988	0	0
AAMBER2	1991-03-10	-64.022	84.529	0	0
KROCK	1993-01-29	-65.983	70.498	1	1
KROCK	1993-01-29	-65.496	70.506	1	1
KROCK	1993-01-29	-64.999	70.509	1	1
KROCK	1993-01-28	-68.497	70.520	0	0
KROCK	1993-01-29	-66.514	70.567	1	1
KROCK	1993-01-26	-65.991	71.995	0	0
KROCK	1993-01-26	-65.007	71.996	0	0
KROCK	1993-01-26	-66.535	72.001	0	0
KROCK	1993-01-26	-65.484	72.004	0	0
KROCK	1993-01-27	-68.474	72.008	0	0
KROCK	1993-01-28	-68.012	72.045	0	0
KROCK	1993-01-26	-64.987	73.473	0	0
KROCK	1993-01-25	-66.498	73.490	0	0
KROCK	1993-01-25	-65.501	73.491	1	1
KROCK	1993-01-22	-68.508	73.491	0	0
KROCK	1993-01-23	-67.502	73.494	0	0
KROCK	1993-01-25	-66.000	73.497	0	0
KROCK	1993-01-24	-66.995	73.497	0	0
KROCK	1993-01-23	-68.007	73.509	0	0
KROCK	1993-01-21	-67.598	74.993	0	0
KROCK	1993-01-21	-66.003	75.001	0	0
KROCK	1993-01-21	-66.976	75.001	0	0
KROCK	1993-01-22	-68.967	75.002	0	0
KROCK	1993-01-22	-68.002	75.002	0	0

KROCK	1993-01-20	-64.999	75.002	0	0
KROCK	1993-01-21	-65.498	75.003	0	0
KROCK	1993-01-22	-68.473	75.014	0	0
KROCK	1993-01-21	-66.477	75.017	0	0
KROCK	1993-01-19	-66.969	76.311	0	0
KROCK	1993-01-20	-65.007	76.502	1	1
KROCK	1993-01-19	-67.497	76.507	0	0
KROCK	1993-01-17	-68.998	76.509	0	0
KROCK	1993-01-18	-68.500	76.510	0	0
KROCK	1993-01-20	-66.019	76.510	0	0
KROCK	1993-01-20	-65.532	76.515	0	0
KROCK	1993-01-20	-66.499	76.518	0	0
KROCK	1993-01-19	-68.013	76.547	0	0
KROCK	1993-01-16	-66.474	77.658	0	0
KROCK	1993-01-15	-65.510	77.997	0	0
KROCK	1993-01-17	-68.002	78.003	0	0
KROCK	1993-01-15	-64.997	78.019	1	1
KROCK	1993-01-16	-66.005	78.024	0	0
BROKE	1996-01-30	-66.022	79.983	1	1
BROKE	1996-02-01	-64.850	79.990	1	1
BROKE	1996-02-02	-63.000	80.002	1	1
BROKE	1996-01-31	-65.732	80.004	0	0
BROKE	1996-02-01	-64.494	80.010	1	1
BROKE	1996-01-31	-65.382	80.035	1	1
BROKE	1996-02-01	-63.991	80.052	1	1
BROKE	1996-02-09	-65.998	93.538	0	0
BROKE	1996-02-08	-64.838	93.539	0	0
BROKE	1996-02-07	-63.600	93.556	0	0
BROKE	1996-02-07	-63.996	93.559	1	1
BROKE	1996-02-06	-63.010	93.560	0	0
BROKE	1996-02-07	-64.281	93.563	1	1
BROKE	1996-02-14	-64.292	104.424	1	1
BROKE	1996-02-14	-64.593	104.428	3	1
BROKE	1996-02-14	-63.912	104.430	1	1
BROKE	1996-02-15	-63.005	104.433	1	1
BROKE	1996-02-15	-63.300	104.435	0	0
BROKE	1996-02-15	-63.594	104.436	0	0
BROKE	1996-02-13	-64.842	104.500	7	1
BROKE	1996-02-13	-65.003	104.668	2	1
BROKE-West	2006-02-17	-61.999	70.000	0	0
BROKE-West	2006-02-17	-63.333	69.990	0	0

BROKE-West	2006-02-18	-64.504	70.010	0	0
BROKE-West	2006-02-19	-65.504	70.000	0	0
BROKE-West	2006-02-20	-66.731	70.000	0	0
BROKE-West	2006-02-20	-66.876	70.000	0	0
BROKE-West	2006-02-20	-67.181	69.990	0	0
BROKE-West	2006-02-23	-61.663	80.000	0	0
BROKE-West	2006-02-25	-63.008	80.020	0	0
BROKE-West	2006-02-26	-64.008	80.010	0	0
BROKE-West	2006-02-26	-64.495	80.000	0	0
BROKE-West	2006-02-26	-65.002	79.990	0	0
BROKE-West	2006-02-26	-65.516	80.000	0	0
BROKE-West	2006-02-27	-65.825	79.990	0	0
BROKE-West	2006-02-27	-65.850	80.000	0	0
BROKE-West	2006-02-27	-66.025	80.000	0	0

[a]For ease of comparison with other studies, *Salpa thompsoni* are reported in both abundances (individuals m^{-2}) and densities (individuals m^{-3}).

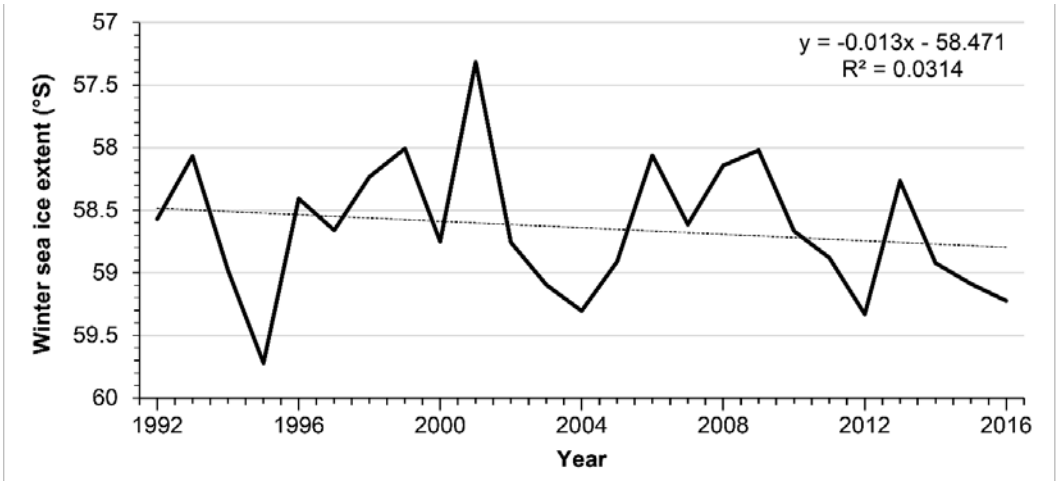


Figure A1.1 1992-2016 average winter sea-ice extent for the region of 70 °E-105 °E, with linear trend.

Table A1.4 One-way ANOVA results, testing statistical significance of linear trend in the 1992-2016 average latitudinal sea-ice extent during winter for the region of 70 °E–105 °E[a].

Model statistics		Model Terms				
Adj. R-sq.	DF	Coefficient	Est.	St. Error	t-value	p-value
-0.011	23	Intercept	-58.471	0.224	-261.281	<0.001
		Year	-0.013	-0.864	-0.864	0.397

[a]Adj. R-sq, adjusted R-squared value, DF, degrees of freedom; Est., estimated effect of variable on temperature; St. Error, standard error.

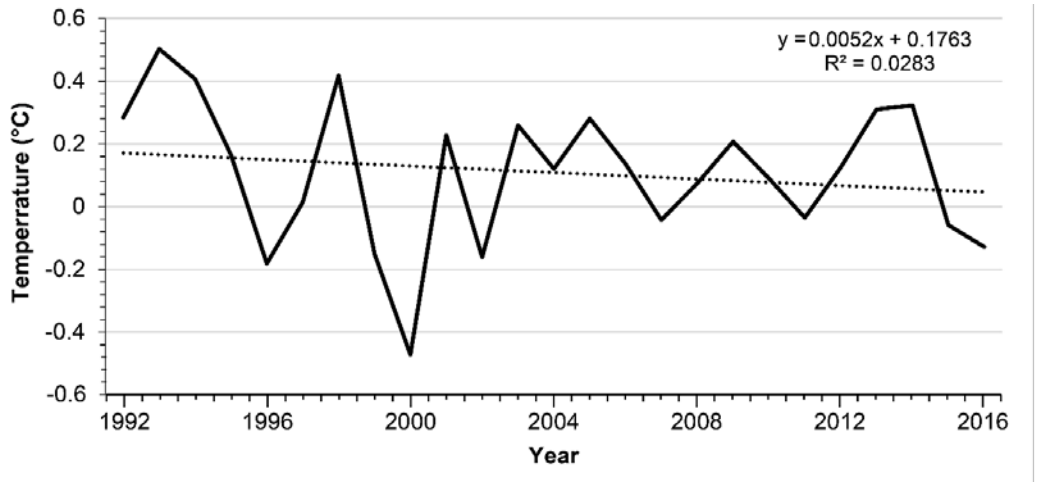


Figure A1.2 1992-2016 average summer Sea Surface Temperature for the region of 70 °E–105 °E, with linear trend.

Table A1.5 One-way ANOVA results, testing statistical significance of linear trend in the 1992-2016 average summer Sea Surface Temperature for the region of 70 °E–105 °E[a].

Model statistics		Model Terms				
Adj. R-sq.	DF	Coefficients	Est.	St. Error	t-value	p-value
-0.014	23	Intercept	0.176	0.094	1.870	0.074
		Year	-0.005	0.006	-0.819	0.421

[a]Adj. R-sq., adjusted R-squared value, DF, degrees of freedom; Est., estimated effect of variable on temperature; St. Error, standard error.

Table A1.6 Variance Inflation Factors (VIF) of continuous environmental variables[a]

Variable	VIF
Time since retreat (weeks)	3.60
Chlorophyll-*a* (mg m^{-2})	1.26
Temperature minimum	2.40
Solar elevation	1.26
Seasonal mixed layer depth (m)	3.22
Salinity	1.39
Buoyancy (N^2)	4.20

[a]VIF >3 indicates high collinearity with at least one other variable.

Table A1.7 Model fit statistics used to identify best explanatory variable from amongst the correlated environmental variables. Model equation: *Salpa thompsoni* abundance (ind. 1,000 m^{-3}) ~ oceanographic zone -1 + s(correlated variable) + s(chlorophyll-*a*) + s(solar elevation)[a,b,c]

Correlated variable	Indicators of model fit			
	DF	AIC	Dev. exp.	R-sq.
Time since retreat (weeks)	10.110	362.644	0.515	0.608
Temperature minimum (°C)	7.000	373.638	0.219	-0.142
Seasonal mixed layer depth (m)	7.000	366.120	0.390	-2.475
Buoyancy (N^2)	7.000	375.407	0.186	-0.065
Salinity	7.000	375.631	0.199	-2.685

[a]Model family is negative binomial with a log link, set to a maximum of 1,000 iterations. [b]DF, degrees of freedom; AIC, Akaike Information Criteria; Dev. exp., deviance explained; R-sq., R-sqaured value. [c]in model equation, s proceeding a variable indicates application of thin-plate smoothing spline.

A2

Tables for Chapter 3: POM stable isotope analysis sampling locations and individual *Salpa thompsoni* and euphausiid elemental and stable isotope composition

Table A2.1 KAXIS POM sampling locations

Size class (µm)	Date	Latitude (°S)	Longitude (°E)
>1.2 um, <210	2016-01-24	-61.80	93.35
>1.2 um, <210	2016-01-24	-61.44	93.46
>1.2 um, <210	2016-01-30	-63.77	82.83
>1.2 um, <210	2016-02-05	-61.94	85.03
>210um <1000	2016-02-05	-61.94	85.03
>1.2 um, <210	2016-02-06	-60.34	82.43
>210um <1000	2016-02-06	-60.34	82.43
>210um <1000	2016-02-07	-58.65	80.14
>1.2 um, <210	2016-02-10	-58.96	84.87
>1.2 um, <210	2016-02-11	-60.07	85.85
>210um <1000	2016-02-11	-60.07	85.85
>1.2 um, <210	2016-02-12	-60.29	83.75
>210um <1000	2016-02-12	-60.29	83.75
>210um <1000	2016-02-13	-60.80	80.39

Table A2.2 KAXIS *Salpa thompsoni* and euphausiid stable isotope analysis sample inventory[a,b].

Taxa	Trawl	Date	Latitude (°S)	Longitude (°E)	Depth (m)	Wet weight (mg)	Dry weight (mg)	C (%)	N (%)	C (mg)	N (mg)
Euphausia frigida	R25	2016-02-06	60.362	82.497	200	44.14	9.26	39.16	9.70	3.63	0.90
						32.08	7.1	37.99	10.47	2.70	0.74
						47.26	9.86	41.42	10.77	4.08	1.06
						44.31	10.32	42.02	9.57	4.34	0.99
						59.58	12.48	41.05	11.4	5.12	1.42
						42.57	8.62	39.96	10.63	3.44	0.92
						35.78	7.69	41.02	10.96	3.15	0.84
						41.67	8.92	40.67	10.58	3.63	0.94
						47.04	9.07	40.53	10.72	3.68	0.97
						57.25	9.74	40.45	11.08	3.94	1.08
						31.17	6.59	40.56	10.34	2.67	0.68
						46.37	8.92	40.21	10.67	3.59	0.95

R38	2016-02-11	60.910	79.882	200	31.53	7.74	40.88	10.63	3.16	0.82
					30.73	6.53	46.18	10.42	3.02	0.68
					58.31	13.05	40.62	10.63	5.30	1.39
					54.99	13.56	38.93	10.36	5.28	1.40
					68.11	14.08	42.33	10.28	5.96	1.45
					60.75	14.4	40.09	10.84	5.77	1.56
					24.15	4.18	42.17	11.23	1.76	0.47
R34	2016-02-10	59.101	84.411	200	57.56	5.69	39.27	9.96	2.23	0.57
					55.06	9.01	46.07	9.89	4.15	0.89
					71.32	6.92	40.07	10.10	2.77	0.70
					56.47	5.59	47.82	9.77	2.67	0.55
					70.79	4.91	46.26	7.95	2.27	0.39
					65.02	5.83	41.31	10.54	2.41	0.61
					68.19	10.33	39.91	10.45	4.12	1.08
					68.94	5.74	40.38	10.27	2.32	0.59

						57.19	8.93	41.16	10.56	3.68	0.94
						82.97	12.23	38.55	9.97	4.71	1.22
						70.08	12.74	37.59	9.29	4.79	1.18
						72.47	11.01	38.40	9.60	4.23	1.06
Euphausia superba	R08	2016-01-27	62.470	87.158	200	1241.22	313.5	46.71	9.4	146.44	29.47
						1533.08	369.23	45	9	166.15	33.23
						644.17	160.96	47.37	8.63	76.25	13.89
						1337.77	342.3	47.32	10.21	161.98	34.95
						1261.92	294.55	41.31	10.54	121.68	31.05
						1059.29	222.88	39.4	10.25	87.81	22.85
						1236.99	255.63	41.37	10.57	105.75	27.02
						1148.25	276.48	47.52	10.18	131.38	28.15
						499.79	113.07	42.71	9.42	48.29	10.65
						353.36	80.21	44.81	8.84	35.94	7.09

R15	2016-02-01	84.769	64.410	200	1309	312.9	47.03	9.61	147.16	30.07
					1584.91	394.48	47.13	10.22	185.92	40.32
					475.45	97.13	43.89	10.22	42.63	9.93
					1465.5	361.83	45.65	9.38	165.18	33.94
					767.02	179.86	42.85	8.91	77.07	16.03
					1231.24	314.8	45	9.13	141.66	28.74
					622.04	146.58	47.79	8.93	70.05	13.09
					852.76	210.26	46.28	8.59	97.31	18.06
R23	2016-02-05	61.936	85.035	200	47.69	11.05	40.52	10.74	4.48	1.19
					1206.17	261.47	46.72	9.20	122.16	24.06
					1061.08	232.72	46.26	7.95	107.66	18.50
					881.83	205.1	46.84	10.91	96.07	22.38
					135.56	26.43	39.91	9.66	10.55	2.55
					1409.09	338.67	49.62	7.36	168.05	24.93
					1090.63	199.7	40.32	9.07	80.52	18.11

	R25	2016-02-06	60.362	82.497	200	635.55	139.36	42.87	9.83	59.74	13.70
						1067.58	231.08	45.46	8.57	105.05	19.80
Euphausia triacantha	R34	2016-02-10	59.101	84.411	200	182.68	44.9	44.42	10.35	19.94	4.65
						179.48	46.93	45.22	9.54	21.22	4.48
						144.91	31.54	41.61	10.18	13.12	3.21
						120.51	28.71	43.95	10.51	12.62	3.02
						151.29	37.04	44.59	10.46	16.52	3.87
						143.22	32.692	43.18	10.20	14.12	3.33
						231.65	59.44	46.39	9.92	27.57	5.90
						197.41	50.44	44.72	8.94	22.56	4.51
						252.38	61.39	46.30	9.24	28.42	5.67
						161.77	40.93	44.75	9.62	18.32	3.94
Thysanoessa macrura	R25	2016-02-06	60.362	82.497	200	107.47	31.67	53.70	7.10	17.01	2.25
						85.88	24.39	48.23	8.60	11.76	2.10

					83.26	22.83	49.82	7.64	11.37	1.74
					286.8	77.03	50.75	7.05	39.09	5.43
					112.87	30.59	50.68	8.35	15.50	2.55
					74.27	22.58	54.46	7.61	12.30	1.72
					103.17	28.27	48.77	7.37	13.79	2.08
					75.33	19.73	49.97	8.20	9.86	1.62
					47.53	12.35	50.94	8.65	6.29	1.07
					74.44	22.59	51.84	7.97	11.71	1.80
R08	2016-01-27	62.470	87.158	200	181.38	61.38	48.22	8.09	29.60	4.97
					100.89	25.22	46.21	8.96	11.65	2.26
					135.78	37.9	56.03	7.19	21.24	2.73
					93.07	26.39	54.98	7.61	14.51	2.01
					98.89	21.48	47.87	8.83	10.28	1.90
					96.89	24.16	50.76	7.91	12.26	1.91
					64.58	12.57	44.51	9.96	5.59	1.25

						68.93	14.14	46.86	8.65	6.63	1.22
						88.4	21.58	51.05	8.69	11.02	1.88
						68.26	15.83	51.62	8.25	8.17	1.31
						30.63	6.35	51.85	9.14	3.29	0.58
						25.75	4.55	48.53	9.76	2.21	0.44
						24.51	5.36	45.43	8.91	2.44	0.48
	R34	2016-02-10	59.101	84.411	200	24.68	6.79	47.76	8.01	3.24	0.54
						90.58	25.56	50.45	7.40	12.90	1.89
						81.63	20.21	49.77	7.62	10.06	1.54
						94.93	27.94	52.12	6.83	14.56	1.91
						33.92	8.36	45.48	8.22	3.80	0.69
						100.14	25.96	48.10	8.33	12.49	2.16
						99.44	22.3	46.70	8.52	10.41	1.90
Salpa thompsoni	R03	2016-01-24	60.362	82.497	200	630.54	36.35	18.97	3.52	6.90	1.28

					871.14	46.57	16.76	3.11	7.81	1.45
					826.81	45.14	21.81	4.07	9.85	1.84
					246.79	15.6	14.86	2.98	2.32	0.46
					214.5	12.41	15.00	2.74	1.86	0.34
					182.75	10.45	14.00	2.60	1.46	0.27
					119.3	6.41	14.28	2.38	0.92	0.15
					81.93	4.82	15.06	2.60	0.73	0.13
					86.79	8.8	39.06	6.50	3.44	0.57
R08	2016-01-27	62.470	87.158	200	166.53	9.51	21.92	4.20	2.08	0.40
					253.63	13.94	20.44	3.62	2.85	0.50
					168.49	8.94	21.10	3.63	1.89	0.32
					205.6	10.66	12.91	2.74	1.38	0.29
					169.02	9.39	22.99	3.69	2.16	0.35
					214.82	11.09	18.35	3.37	2.04	0.37
					43.19	2.38	18.90	3.28	0.45	0.08

					459.41	23.37	16.63	2.91	3.89	0.68
					235.27	11.88	14.83	2.89	1.76	0.34
					324.71	16.29	19.44	3.74	3.17	0.61
					321.25	17.54	18.63	3.53	3.27	0.62
					510.94	29.28	19.07	3.76	5.58	1.10
					391.81	23.1	15.65	3.46	3.62	0.80
					624.44	18.91	19.15	3.48	3.62	0.66
					323.05	16.97	19.54	3.00	3.32	0.51
					295.65	14.78	22.16	3.51	3.28	0.52
					520.06	26.85	19.01	3.28	5.10	0.88
R12	2016-01-29	63.292	82.042	200	1134.91	76.74	18.85	4.31	14.47	3.31
					1032.17	67.36	20.52	4.66	13.82	3.14
					417.22	22.98	15.58	3.51	3.58	0.81
					507.17	32.53	16.76	3.81	5.45	1.24
					796.64	51.44	18.02	3.16	9.27	1.63

					279.58	16.93	20.70	3.83	3.50	0.65
					164.46	9.27	17.54	3.28	1.63	0.30
					502.06	30.64	23.88	4.80	7.32	1.47
					135.77	7.67	17.74	3.38	1.36	0.26
					57.44	3.26	23.05	4.28	0.75	0.14
R13	2016-01-20	63.930	83.065	200	511.98	33.4	22.28	4.67	7.44	1.56
					310.24	17.6	20.34	4.11	3.58	0.72
					546.95	33.7	21.30	4.35	7.18	1.47
					633.45	35.99	20.37	4.21	7.33	1.52
					461.72	25.37	16.21	3.03	4.11	0.77
					656.4	99	21.23	4.28	21.02	4.24
					867.94	49.67	20.00	4.31	9.93	2.14
					1003.36	45.23	12.05	2.40	5.45	1.09
					787.75	43.4	21.12	4.63	9.17	2.01
					609	31.91	17.06	3.07	5.44	0.98

R15	2016-02-01	64.410	84.769	200	494.84	26.81	16.00	3.18	4.29	0.85
					205.85	10.88	20.15	3.93	2.19	0.43
					607.47	32.98	17.53	3.08	5.78	1.02
					867.15	45.49	16.79	3.02	7.64	1.37
					102.95	5.87	19.24	3.57	1.13	0.21
					583.05	31.71	16.13	3.24	5.11	1.03
					121.3	6.7	13.30	2.36	0.89	0.16
					75.2	4.5	24.53	4.58	1.10	0.21
R23	2016-02-05	61.936	85.035	200	110.82	6.37	19.34	3.60	1.23	0.23
					225.1	12.61	16.60	3.32	2.09	0.42
					273.67	13.85	19.38	3.56	2.68	0.49
					179.39	8.94	17.11	3.35	1.53	0.30
					279.36	15.68	16.46	3.06	2.58	0.48
					168.98	8.21	12.93	2.45	1.06	0.20
					296.41	16.21	17.27	3.53	2.80	0.57

					388.72	21.96	18.09	3.64	3.97	0.80
					127.24	6.96	15.95	2.95	1.11	0.21
R38	2016-02-11	60.910	79.882	200	170.81	8.39	18.68	3.40	1.57	0.29
					330.28	18.11	14.66	2.60	2.65	0.47
					373.74	20.25	17.12	2.86	3.47	0.58
					164.02	8.82	17.69	3.00	1.56	0.26
					193.83	11.11	15.95	2.92	1.77	0.32
					197.86	10.96	18.71	3.09	2.05	0.34
					231.68	10.75	11.92	2.41	1.28	0.26
					196.08	11.04	17.24	3.13	1.90	0.35
					44.13	2.28	25.14	4.31	0.57	0.10
					287.14	14.52	14.98	2.51	2.18	0.36
					40.13	1.31	17.52	3.75	0.23	0.05
					599.51	32.13	18.07	3.32	5.81	1.07
					661.9	33.29	15.32	3.20	5.10	1.07

R34	2016-02-10	59.101	84.411	200	10.93	0.46	6.88	1.22	0.03	0.01
					438.46	23.95	21.13	5.57	5.06	1.33
					412.77	26.23	25.55	7.04	6.70	1.85
					227.201	14.131	24.03	6.68	3.40	0.94
					389.08	21.24	16.87	3.09	3.58	0.66
					473.72	28.22	27.89	8.11	7.87	2.29
					428.37	25.76	19.90	4.58	5.13	1.18
					369.89	20.76	18.53	3.25	3.85	0.67
					377.2	22.73	19.20	4.50	4.36	1.02
					55.11	2.05	6.90	1.24	0.14	0.03

[a]C, carbon; N, nitrogen.

[b]all trawls are routine trawls.

Table A2.3 Breakdown of *Salpa thompsoni*/*Euphausia superba* routine trawl density overlap, illustrated in Fig 3.3[a]

		Salpa thompsoni (individuals 1,000 m^{-3})		
	No. 1 ° x 1 ° cells	Low (0-100)	Medium (101-1,000)	High (1,001-2,500)
Euphausia superba (individuals 1,000 m^{-3})	Low	164	23	2
	Medium	6	1	1
	High	1	1	0

[a]"Low," "Medium," and "High" classifications are based on the overall density trends across the ~35 years of routine trawl data used in this study. They are not based on external population metrics or density records.

A3

Tables for Chapter 4: Trawl register for KAXIS *Salpa thompsoni* morphometrics and elemental and energetic analysis, and individual elemental (*Salpa thompsoni*) and energetic (*Salpa thompsoni* and *Euphausia superba*) profiles

Table A3.1 Routine (R) and Target (T) trawl register[a,b,c]

Trawl	Date/Time (UTC)	Lat (°)	Lon (°)	Metrics	*S. thompsoni* aggregate community composition
R00	2016-01-22T07:31:18	-65.455	93.181	MM	Imm. =3
R03	2016-01-24T07:44:31	-61.718	93.327	MM, CN	Imm.=4, Dev.=1, Mat.=9
R05	2016-01-25T07:16:47	-61.976	92.536	MM	Imm.=22
R08	2016-01-27T07:44:28	-62.470	87.158	MM, CN	Imm=1, Dev.=11, Mat.=21
R10	2016-01-28T07:21:12	-62.530	83.905	MM	Imm.=14
R12	2016-01-29T20:20:58	-63.292	82.042	MM, CN	Dev.=2, Mat.=2
R13	2016-01-20T11:08:06	-63.930	83.065	MM, CN	Imm.=1, Dev.=8, Mat.=24
R15	2016-02-01T05:30:30	-64.410	84.769	MM	Imm.=16, Dev.=44, Mat.=39
T14	2016-02-01T23:55:17	-65.166	85.769	KN	
R18	2016-02-02T21:50:00	-65.042	91.494	MM, CN	Dev.=2, Mat=1

T16	2016-02-03T17:38:55	-63.987	89.124	KN	
R23	2016-02-05T11:23:00	-61.936	85.035	MM, CN	Imm.=14, Dev.=42, Mat.=24
R26	07.02.16T09:14:51	-59.344	81.073	MM	Imm.=3
R28	08.02.16T10:19:07	-58.223	81.912	MM	Imm.=13, Dev.=54, Mat.=12
R30	09.02.16T10:05:07	-57.608	84.609	MM	Imm.=17, Dev.=28, Mat.=6
R31	09.02.16T10:01:54	-57.838	85.290	MM, SN	Imm.=31, Dev.=13, Mat.=5
R32	10.02.16T07:57:34	-58.875	85.141	MM	Imm.=7, Dev.=2
R34	10.02.16T16:21:14	-59.101	84.411	MM, CN	Imm.=24, Dev.=24, Mat.=2
T25	12.02.16T04:34:00	-60.180	84.731	SN	
R38	13.02.16T15:03:58	-60.910	79.882	MM, CN	Imm.=14, Dev.=64, Mat.=1
R40	15.02.16T01:28:00	-61.846	74.115	MM	Imm.=12, Dev.=42, Mat.=5
R42	15.02.16T10:46:59	-62.704	73.314	MM	Imm.=6, Dev.=59, Mat.=15

[a] Date follows dd:mm:yy format, and time hh:mm:ss.

[b] MM, *S. thompsoni* morphometrics; CN, *S. thompsoni* carbon and nitrogen; SN, *S. thompsoni* nutritional profile; KN, krill nutritional profile.

[c] Imm., immature aggregate; Dev., Developing aggregate; Mat., mature aggregate.

Table A3.2 *Salpa thompsoni* morphometrics and cabon (C) and nitrogen (N) content[a,]

Trawl	TL (mm)	OAL (mm)	Maturity Stage	WW (mg)	DW (mg)	C (%DW)	N (%DW)
R03	26.00	22.04	Dev.	871.14	46.57	16.76	3.11
R03	50.60	35.95	Mat.	630.54	36.35	18.97	3.52
R03	63.27	44.92	Mat.	826.81	45.14	21.81	4.07
R03	63.27	44.92	Mat.	119.30	6.41	14.28	2.38
R03	59.57	47.44	Mat.	246.79	15.60	14.86	2.98
R03	50.60	35.95	Mat.	214.50	12.41	15.00	2.74
R03	63.29	52.98	Mat.	182.75	10.45	14.00	2.60
R03	77.77	71.68	Mat.	81.93	4.820	15.06	2.60
R03	61.73	45.17	Mat.	86.79	8.80	39.06	6.50
R08	31.81	20.99	Dev.	166.53	9.51	21.92	4.20
R08	28.36	19.36	Dev.	168.49	8.94	21.10	3.63
R08	26.77	19.01	Dev.	205.60	10.66	12.91	2.74

R08	32.09	20.48	Dev.	214.82	11.09	18.35	3.37
R08	37.52	23.44	Dev.	235.27	11.88	14.83	2.89
R08	37.12	23.86	Dev.	324.71	16.29	19.44	3.74
R08	19.36	12.83	Imm.	43.19	2.38	18.90	3.28
R08	33.86	25.54	Mat.	253.63	13.94	20.44	3.62
R08	47.65	29.31	Mat.	459.41	23.37	16.63	2.91
R08	32.67	26.1	Mat.	321.25	17.54	18.63	3.53
R08	35.70	27.01	Mat.	510.94	29.28	19.07	3.76
R12	47.71	24.48	Dev.	164.46	9.27	17.54	3.28
R12	50.94	20.98	Dev.	135.77	7.67	17.74	3.38
R12	27.35	14.89	Dev.	57.44	3.26	23.05	4.28
R12	64.52	52.54	Mat.	1134.91	76.74	18.85	4.31
R12	68.85	56.49	Mat.	1032.17	67.36	20.52	4.66
R12	44.19	38.14	Mat.	417.22	22.98	15.58	3.51
R12	52.77	43.93	Mat.	507.17	32.53	16.76	3.81
R12	52.00	46.78	Mat.	796.64	51.44	16.84	3.31
R12	61.49	57.94	Mat.	506.91	31.20	19.15	3.48
R12	65.40	35.28	Mat.	279.58	16.93	20.70	3.83
R12	56.58	32.34	Mat.	502.06	30.64	23.88	4.80
R13	37.07	19.08	Dev.	310.24	17.60	20.34	4.11
R13	48.12	29.5	Mat.	511.98	33.40	22.28	4.67
R13	51.50	31.91	Mat.	546.95	33.70	21.30	4.35
R13	51.05	26.09	Mat.	633.45	35.99	20.37	4.21
R13	44.00	31.19	Mat.	461.72	25.37	16.21	3.03
R13	48.72	33.75	Mat.	656.40	99.00	21.23	4.28
R13	55.82	34.52	Mat.	867.94	49.67	20.00	4.31
R13	56.70	30.8	Mat.	1003.36	45.23	12.05	2.40
R13	67.98	31.14	Mat.	787.75	43.40	21.12	4.63
R13	47.64	26.06	Mat.	609.00	31.91	17.06	3.07
R15	44.73	24.15	Dev.	607.47	32.98	17.53	3.08
R15	26.70	15.54	Dev.	75.20	4.50	24.53	4.58
R15	39.55	20.66	Dev.	205.85	10.88	20.15	3.93
R15	51.67	21.9	Dev.	494.84	26.81	16.00	3.18
R15	29.19	14.47	Imm.	102.95	5.87	19.24	3.57
R15	62.31	27.32	Mat.	583.05	31.71	16.13	3.24
R15	61.73	29.22	Mat.	867.15	45.49	16.79	3.02
R23	41.90	20.45	Dev.	225.10	13.85	19.38	3.56
R23	36.00	19.66	Dev.	279.36	8.94	17.11	3.35
R23	52.34	15.42	Dev.	273.67	15.68	16.46	3.06
R23	30.69	15.7	Dev.	168.98	8.21	12.93	2.45
R23	39.49	18.82	Dev.	296.41	16.21	17.27	3.53
R23	55.75	21.87	Dev.	767.02	179.86	18.09	3.64
R23	31.89	14.37	Imm.	110.82	6.37	19.34	3.60

R23	27.89	13.59	Imm.	179.39	12.61	16.60	3.32
R23	30.21	13.84	Imm.	127.24	6.96	15.95	2.95
R34	39.34	21.64	Dev.	389.08	21.24	16.87	3.09
R34	40.57	23.73	Dev.	412.77	26.23	25.55	7.04
R34	35.60	17.99	Dev.	438.46	23.95	21.13	5.57
R34	18.05	9.43	Imm.	33.02	1.26	6.88	1.22
R34	42.19	38.26	Mat.	377.20	22.73	19.20	4.50
R34	51.16	48.7	Mat.	428.37	25.76	19.90	4.58
R34	57.31	55.04	Mat.	473.72	28.22	27.89	8.11
R34	36.36	31.05	Mat.	227.20	14.13	24.03	6.68
R34	44.75	25.01	Mat.	369.89	20.76	18.53	3.25
R38	50.75	20.27	Dev.	170.81	8.39	18.68	3.40
R38	61.28	22	Dev.	330.28	18.11	14.66	2.60
R38	57.58	19.82	Dev.	373.74	20.25	17.12	2.86
R38	46.94	16.61	Dev.	164.02	8.82	17.69	3.00
R38	55.42	15.75	Dev.	193.83	11.11	15.95	2.92
R38	44.67	17.51	Dev.	197.86	10.96	18.71	3.09
R38	51.50	22.6	Dev.	231.68	10.75	11.92	2.41
R38	47.53	15.59	Dev.	196.08	11.04	17.24	3.13
R38	45.55	22.6	Dev.	44.13	2.28	25.14	4.31
R38	51.85	15.59	Dev.	287.14	14.52	14.98	2.51

[a]TL, total length; OAL, oral-atrial length; WW, wet weight; DW, dry weight; Imm., immature; Dev., developing; Mat., mature.

Table A3.3 Individual *Salpa thompsoni* and *Euphausia superba* nutritional profiles[a].

Species	Trawl	Maturity Stage	WW (mg)	DW (mg)	Protein (%DW)	Joules ind^{-1}
S. thompsoni	R31	Dev.	36.25	2.17	7.21	
	R31	Mat.	513.93	30.84	5.32	45.99
	R31	Mat.	333.47	20.01	7.80	33.15
	R31	Mat.	277.45	16.65	8.61	16.12
	R31	Mat.	298.12	17.89	1.74	
	R31	Mat.	165.15	9.91	9.42	
	R31	Dev.	34.66	2.08	6.19	
	T25	Mat	343.84	21.32	9.53	25.34
	T25	Mat.	337.58	20.93	4.79	
	T25	Mat.	111.66	6.92	10.31	
	T25	Mat.	411.55	25.52	9.63	
	T25	Mat.	186.39	11.18		15.12
	T25	Mat.	233.98	14.04		33.42
	T25	Mat.	444.11	26.65		30.88
	T25	Mat.	144.26	8.66	7.68	13.08

E. superba	T14	Adult M	991.1	228.94	43.20	4036.48
	T14	Adult M	916.24	211.65	51.95	2604.24
	T14	Adult M	934.04	215.76	37.46	4086.51
	T14	Adult M	890.04	205.60	49.96	3214.73
	T14	Adult M	1015.22	234.52		3143.78
	T14	Adult M	1125.01	259.88	39.48	3762.88
	T14	Adult M	969.91	145.78	45.53	
	T14	Adult M	851.58	148.48	28.76	
	T14	Juvenile	175.08	24.52	26.78	
	T16	Adult M	507.22	108.38	44.37	
	T16	Adult M	524.18	121.09		2082.62
	T16	Adult M	607.61	140.36		2749.33
	T16	Adult M	439.31	89.32	48.60	1816.53
	T16	Adult M	506.39	152.7	54.10	2233.95
	T16	Adult M	543.51	125.55		2418.75
	T16	Adult M	330.48	56.46	34.59	
	T16	Adult M	543.51	105.37	30.87	
	T16	Adult M	290.43	67.09	55.28	

[a]WW, wet weight; DW, dry weight

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